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CONTRIBUTIONS TO THE LICHEN FLORA OF INDIA AND NEPAL

I. The Genus *Physcia* (Ach.) Vain.

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Introduction

In spite of an abundance of variety in the lichen flora conforming to the various climatic and phytogeographic regions of India and its geographically contiguous Himalayan territory of Nepal, our knowledge of it is yet considerably poor. The remarks, "the Lichenology of India has only been very partially investigated; indeed, with the exception of a hurried survey of the part of Nilgherries, two or three nuclei so to speak, in the neighbourhood of large towns, and Sir J. D. Hooker's collections from the southern slope and spurs of the Himalayas the whole may be said in this respect to be *terra incognita*", by Stirton in 1879 largely remain applicable even today. A perusal of the literature on Indian lichens has revealed that even less than a thousand species have so far been reported from this area. A large number of these reports, based as above on scattered collections, by various foreign botanists, belong to the 19th century, while only meagre additions have been made subsequently. The type specimens or even the duplicates of the majority of all such older collections are not present in India. Those preserved are only few fragmentary collections such as of T. Thomson, S. Kurz, Skoliezka and G. Watt in the Calcutta herbarium and of R. Strachey and Winterbottom in the Dehra Dun herbarium. Thus the paucity of authentic specimens, coupled with the meagre classical literature on lichens available in India, may well be considered the reasons to be attributed to our restricted knowledge of lichens in India in the past and may still act as a handicap for a rapid progress in future.

Having been engaged, for over a decade now, with the collections of lichens from different parts of India, particularly from the Himalayan region and Nepal and their taxonomic investigations, fairly large number of species under many a genera are now available with me to

warrant a publication on these investigations. The present contributions are thus based primarily on the lichen collections preserved in my private herbarium. Any other sources from which specimens have been received have been suitably indicated. The information on earlier reports of the individual species under each genus from India has also been incorporated with a view to consolidate as far as possible all the information and references about them. However, they have probably to be used with reservation as most of them may be in need of revision due to the greatly advanced present-day concept of lichen systematics.

For the systematic position, detailed description and the circumscription of the genera to be treated in these contributions, one is advised to refer to the system of Zahlbruckner (1926) and (1922–40) which is adopted by almost all the lichenologists the world over and has been followed here as well. I have attempted to give only short descriptions of the genera so that it acts as a ready reference.

The behaviour of the different species towards the well-known chemicals used in lichenology has been studied. The positive reactions of colour changes are stated after the *plus* (+) symbol while a negative reaction of colour change is represented by a *minus* (—) symbol. The abbreviations used in this respect or otherwise correspond as follows:—

K = aqueous solution of potassium hydroxide; Cl = aqueous solution of calcium hypochlorite; K (Cl) = K followed by Cl; Pd = freshly prepared alcoholic solution of paraphenylenediamine; I = aqueous solution of iodine (in a little potassium iodide); DDA = D. D. Awasthi. The numbers within parenthesis in the details of the specimens refer to its serial number in Herbarium D. D. Awasthi or else the location or source of the specimen is indicated. Hb. Cal. = Herbarium, Indian (Royal) Botanic Garden, Calcutta.

Investigations are now complete on the small family Physciaceæ which comprises the three genera—*Pyxine*, *Physcia* and *Anaptychia* which are distinguished from each other on the basis of the nature of upper cortex of thallus, the nature of apothecia and the K-reaction in the epithecium, as detailed below:—

A. Upper cortex of thallus of conglutinate vertical hyphæ (paraplectenchymatous in section)

B. Apothecia lecideine (or ultimately lecideine), epithecium K+violet-purple .. *Pyxine*

BB. Apothecia lecanorine, epithecium K— .. *Physcia*

AA. Upper cortex of longitudinally disposed conglutinate hyphæ (not paraplectenchymatous in section), apothecia lecanorine, epithecium K— .. *Anaptychia*

The genus *Physcia* is being treated in the following pages while the results of the investigations on *Anaptychia* and *Pyxine* will follow in this series genus after genus.

ACKNOWLEDGEMENTS

I take this opportunity of expressing my gratitude to Prof. S. N. Das-Gupta for guidance in the prosecution of this work and to Dr. A. H. Magnusson (Sweden) for constant encouragement and help in the verification of many specimens dealt with here. I owe special thanks to Prof. O. A. Hφeg, Fr. G. Foreau and other friends who have kindly presented me their collections of lichens from various parts of India, enriching my lichen herbarium and enabling me to make this study more comprehensive. My thanks are also due to Prof. T. S. Sadasivan for kindly presenting me a set of identified Swedish lichens which facilitated my comparison work.

Physcia (Ach.) Vain.

(Ach. in *Kgl. Vetensk-Akad. Nya Handl.*, **15**, 1794, p. 252), Vain. in *Étud. Lich. Brêsil*, **1**, 1890, p. 138; A. Zahlbr. in Engl. & Prantl, *Natürl. Pflazenfam.* 2 *Auf.* **Bd. 8,** 1926, p. 257.

Thallus foliose, dorsiventral, horizontal to rarely suberect, with rhizinæ on underside. Both sides corticated; upper cortex of vertical conglutinate hyphæ—paraplectenchymatous; lower cortex usually of longitudinally disposed hyphæ, rarely paraplectenchymatous. Medulla white or coloured. Apothecia rounded, sessile, lecanorine. Epithecium K—, hypothecium dark-brown or pale to colourless. Asci 8-spored; spores brown, 2-celled, rarely 4-celled or muriform. Paraphyses simple, septate.

The genus is cosmopolitan in distribution and occurs on substrata —soil, mosses, stones or bark. Over 175 species are known from the world. Previously seventeen species were known from India and the present studies add five more new reports for the area dealt with making the total of species known to twenty-two.

Key to the species

A—Hypothecium brown to dark-brown. Sect. ***Dirinaria***

1 *a*—Thallus sorediate and non-isidiate.

2 *a*—Soralia as verrucæ with coarse granular isidia-like soredia; spores 12–20 × 6–8 μ in size. 1. *Ph. aspera*

2 *b*—Soralia globose farinose, spores 18–21 × 8–10 μ. 2. *Ph. picta*

2 *c*—Soralia cupuliform, towards centre of thallus, laciniæ applanate. white. 3. *Ph. applanata*

1 *b*—Thallus sorediate and isidiate. 2. *Ph. picta* var. *isidiophora*
1 *c*—Thallus neither sorediate nor isidiate. 4. *Ph. aegiliata*

B—Hypothecium colourless to pale. Sect. ***Euphyscia***

3 *a*—Thallus sorediate and non-isidiate.

4 *a*—Medulla yellow ochraceous, K+purple. 5. *Ph. endoxantha*

4 *b*—Medulla colourless.

5 *a*—Thallus pruinose, soralia marginal, pale-greyish. 6. *Ph. detersa*

5 *b*—Thallus epruinose.

6 *a*—Soredia granular, lower cortex of thallus plectenchymatous. 7. *Ph. tribacea*

6 *b* Soredia bluish-white, lower cortex of longitudinally disposed hyphæ. 8. *Ph. caesia*

3 *b*—Thallus neither sorediate nor isidiate.

7 *a*—Medulla coccineus, K + violet-purple. 9. *Ph. endococcina*

7 *b*—Medulla colourless.

8 *a*—Thallus pruinose.

9 *a*—Growing on bark.

10 *a*—Thallus ashy-grey to brownish, laciniæ up to 2 mm. broad, spores 22–36 × 15–18 μ. 10. *Ph. pulverulenta*

10 *b*—Thallus glaucous white, lobes 2–5 mm. broad, spores 24–32 × 10–13 μ. 11. *Ph. askotensis*

9 *b*—Growing on soil or ground.

11 *a*—Thallus blue-grey, central laciniæ ascendent. 12. *Ph. muscigena*

11 *b*—Thallus greenish-grey, laciniæ appressed convex. 13. *Ph. sikkimensis*

8 *b*—Thallus not pruinose.

12 *a*—Laciniæ marginally ciliate.

13 *a*—Medulla K + red; thallus rusty red-brown, cilia black. 14. *Ph. rubricosa*

13 *b*—Medulla K—, thallus grey-brown, cilia greyish-white. 15. *Ph. hispida*

12 *b*—Laciniæ not ciliate marginally.

14 *a*—Lower side black or brown with similar coloured rhizinæ.

15 *a*—Laciniæ discrete throughout, even though superposed.

16 *a*—Laciniæ brown-black, concave canaliculate above, rhizinæ short dense and hirsute. 16. *Ph. melanotricha*

16 *b*—Laciniæ grey-brown, plane, rhizinæ dense-black smooth, apothecia with black cilia at base, spores 20–30 × 10–12 μ. 17. *Ph. setosa*

16 *c*—Laciniæ blue-grey to ashy grey-brown on underside, rhizinæ not dense. 18. *Ph. albonigra*

15 *b*—Laciniæ confluent in the centre, adpressed, glaucous white, spores 22–28 × 9–12 μ. 19. *Ph. integrata*

14 *b*—Lower side pale-grey, rhizinæ also grey.

17 *a*—Thallus white maculate on upper side, spores 20–26 × 8–12 μ. 20. *Ph. aipolia*

17 *b*—Thallus not maculate on upper side.

18 *a*—Thallus whitish, fragile, pale on under side. 21. *Ph. alba*

18 *b*—Thallus stellate greyish-white, underside whitish pale-grey, spores 16–20 × 8–11 μ. 22. *Ph. stellaris*

Sect: ***Dirinaria*** (Tuck.) Vain.; A. Zahlbr. (*l.c.*) p. 257.

The section is characterised by the dark to dark-brown colour of the hypothecium and in this respect is closely allied to the genus *Pyxine*. This similarity is more pronounced with species like *Pyxine berteriana* (Fée) Imshaug (syn. *P. meissneri* Tuck.) in which there is often a lecanorine apothecium, especially in the young stages. The distinction between the two genera in such cases is then limited to the K-reaction in the epithecium. Consequently it (*Dirinaria*) has sometimes been referred under *Pyxine* or considered as a distinct genus as done by Clements (1909, 1931) and recently supported by Imshaug (1957). However, it may probably continue to be treated under *Physcia* 'in view of common usage' following Lynge (1923) and Zahlbruckner (1926, 1931).

1. ***Physcia aspera*** H. Magn. (Plate I, Fig. 1).

A. H. Magn. and A. Zahlbr. in *Arkiv för Bot.* **Bd. 32 A** (2), 1945, p. 63.

Thallus foliose, suborbicular, often growing to large dimensions, adpressed, laciniate. Laciniæ centrally confluent and indistinct individually but discrete at the periphery and then up to 1·5 mm. in width. Thallus rarely subcrustaceous in the central part, sometimes the whole thallus very thin and adglutinate to the bark and often longitudinally rugose in the peripheral region. Thallus above glaucous-grey to ash-grey, sorediate; soredia as verrucæ in the peripheral lobes but centrally 'bursting cratæriform' with a constricted base and often

irregular in outline and with whitish to concolorous granular isidia-like soredia. Often soralia confluent appearing as continuous coarsely granular patches up to 2 mm. in size, sometimes the soralia of the whole thallus more or less confluent. Lowerside of thallus dark-brown to black.

Thickness of the thallus much variable, average 300 μ thick. Upper cortex about 20 μ thick, paraplectenchymatous, of thin-walled vertical hyphæ. Algal stratum continuous, 35-40 μ thick, algal cells green, 8–10 μ in size. Medulla colourless of loosely $\pm$ longitudinally disposed granular surfaced hyphæ; lower cortex brown-black.

Thallus K + yellow, Cl —, K (Cl) —, Pd —.

Apothecia superficial, sessile, crowded or dispersed, often embedded by the sorediate verrucæ, 0·5–1 (1·5) mm. in diameter; disc brown-black to black, plane, rarely scarcely reflexed; margin thalline, entire, crenate to sulcate. Thecium variable in thickness from 60–100 μ, brownish-yellow in the uppermost $\pm$ 10 μ and colourless to pale below, I + blue, K —; hypothecium brown-black, lenticular and tapering marginally, thickness in the middle part varying from 120–160 μ. Asci clavate, 8-spored; spores brown, 2-celled, ellipsoid 12–20 (24) × (4) 6–8 (9) μ in size, not constricted at the septum, wall thickened at the ends (Text-Fig. 2). Paraphyses dense, conglutinate, 1·5–2 μ thick.

Habitat.—Usually on bark of trees, sometimes over stones.

Localities.—N.W. Himalayas, Almora district, alt. 5,000 ft., 1950, DDA and A. M. Awasthi (No. 567); Askote alt. 5,500 ft., 1954, DDA (No. 2694); 1955 (No. 3292); near Tanakpur Kali river valley, on way to Purnagiri, alt. 1,500–2,000 ft., 1955, DDA (Nos. 3181, 3182), 1956 (No. 3381); Dehra Dun, T. R. Seshadri, 1953, (No. 3398); Dehra Dun, P. N. Mehra, 1950 (in Herb. Magnusson); Mohanpass, T. R. Seshadri, 1953 (No. 3729), Nainital district, 1956, T. R. Seshadri, No. A 43, (No. 3603).

South India.—Travancore, Quilon, 1953, O. A. Hφeg (Nos. 2594 and 2596).

E. Nepal, Biratnagar, alt. 1,000 ft., 1949, DDA and D. Chilkoti (No. 510); Barachhetra, Kosi river valley, alt. 1,500 ft., 1949, DDA and D. Chilkoti (No. 530); Phenikhola valley below Phidim, alt. 2,500 ft., 1953, DDA (No. 2172 and 2177–over stone); above Shimboa between Mokhtara and Angbung, alt. 3,000 ft, 1953, DDA. (No. 2478).

Variations in the size and nature of soredia are often noticeable. Sometimes they are very small and densely diffused and may be mistaken for *Ph. picta*. But even in such types the peripheral lobes possess the typical granular soredia and the two species—*Physcia aspera* and *Ph. picta* can easily be separated apart by the granular soredia on a cratæriform soralium in the former and minute globose farinose type in the latter.

The species occurs widely distributed in the tropical and subtropical regions of India. On the tree trunks in the *terai* area, especially on trunks of *Shorea robusta* it forms large grey to glaucous white conspicuous patches even seen from a distance.

Physcia aspera H. Magn. var. ***alutacea*** H. Magn. nov. var. A typo differt thallus alutaceous.

Thallus foliose, adpressed, centrally cracked to somewhat subcrustaceous, plicate rugose longitudinally. Thallus above yellowish-pale to grey-pale, granular sorediate; soralia dispersed throughout the thallus, up to 0·5 mm. in size. Thallus about 300 μ thick; upper cortex 20 μ thick; algal stratum 40 μ thick; medulla colourless of smooth hyphæ; lower cortex brown-black. Thallus K + yellow.

Apothecia numerous, crowded in the central region, sessile, 1–1·5 mm. in diameter; disc plane, black; margin thick, thalline. Thecium brown-black in the uppermost part; hypothecium brown-black, 200 μ in the middle part, sharply defined below and gradually merging into thecium above. Asci 80 × 14 μ, 8-spored; spores brown, 2-celled ellipsoid 16–22 × 6–8 μ in size.

Habitat: On bark of *Shorea robusta* tree.

Locality: *E. Nepal*, Phenikhola valley, below Phidim, alt. 2,500–3,000 ft., D. D. Awasthi, 19–5–1953 (No. 2168 in Hb. *meo*)—TYPE.

2. ***Physcia picta*** (Sw.) Nyl. (Plate I, Fig. 3).

In *Mêmoir Soc. Imp. Science. Natur. Cherbough*, **3**, 1855, p. 175; A. Zahlbr. in *Catal. Lich. Univ.* **7**, 1931, p. 582—*Lichen pictus* Sw. in *Nova Gener.* et *Spec. Plant.* 1788, p. 146.

Thallus foliose, suborbicular, adpressed to the bark, 4–5 cm. in size, centrally ultimately ± subcrustaceous; laciniæ discrete only at the periphery and 1–1·5 mm. broad, confluent centrally, longitudinally plicate rugose. Thallus above ash-grey to greyish pale, sorediate; soralia globose farinose, up to 0·5 mm. in size; lower side black erhizinose.

Thallus ± 160 μ thick; upper cortex 12–15 μ thick, paraplectenchymatous; algal stratum 20–25 μ thick, algal cells 10–12 μ in size. Medulla white, hyphæ 3–4 μ thick.

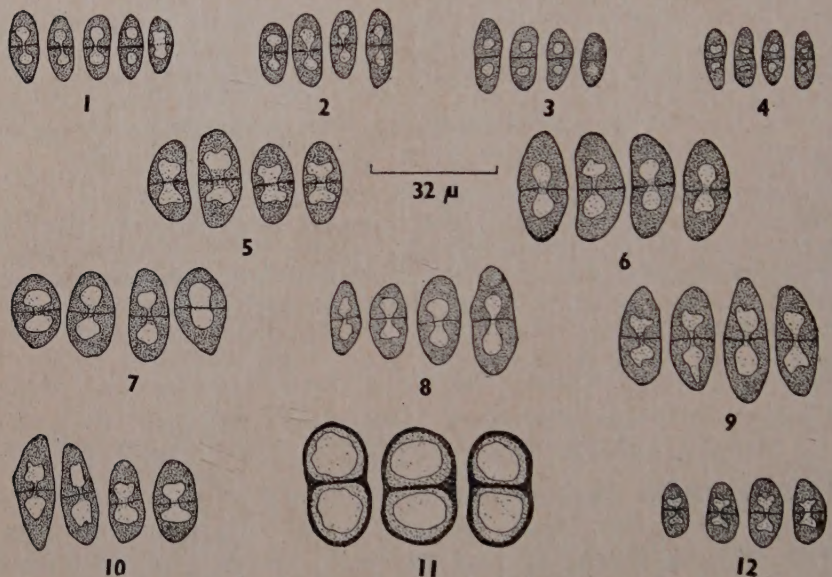
Thallus K + yellowish, Cl — K (Cl) —, Pd—.

Apothecia scarce, up to 1 mm. in diameter, superficial, sessile; disc plane, brown-black; margin thick (180–200 μ), thalline. Thecium 100 μ thick, brownish in the uppermost region, I + blue, K — : hypothecium dark-brown, 140 μ thick in the middle and tapering towards margin. Asci 8-spored; spores dark-brown, 2-celled, ellipsoid, 18–21 × 8–10 μ in size (Text-Fig. 3).

Habitat.—On bark of trees.

Localities.—E. Himalayas; Assam, Silghat, 1957, G. Panigrahi, No. 5400 (Herb. Botanical Survey of India, Shillong and a duplicate in herb. DDA).

N. W. Himalayas; Almora, alt. 5,200 ft., 1949, D. N. Pant (No. 433); Dehra Dun, T. R. Seshadri, No. A21, 1954 (No. 3399). *E. India*, Bengal, Port Canning, 1947, DDA (No. 372).



TEXT-FIGS. 1–12. To show the types of spores in the various species of *Physcia* worked out. Spores of: Fig. 1. *Physcia aegiliata* (Ach.) Nyl. Fig. 2. *Ph. aspera* H. Magn. Fig. 3. *Ph. picta* (Sw.) Nyl. Fig. 4. *Ph. picta* var. *endochroma* H. Magn. et Awasthi. Fig. 5. *Ph. aipolia* (Ehrht.) Hampe. Fig. 6. *Ph. askotensis* Awasthi. Fig. *Ph. endoccocina* (Körb.) Th. Fr. Fig. 8. *Ph. integrata* Nyl. Fig. 9. *Ph. endococcina* var. *latiloba* H. Magn. Fig. 10. *Ph. setosa* (Ach.) Nyl. Fig. 11. *Ph. pulverulenta* var. *argyphaea* (Ach.) Nyl. Fig. 12. *Ph. stellaris* (L.) Nyl.

Earlier Reports

From Calcutta, coll. S. Kurz (Nylander, 1867, p. 3); Calcutta and Andamans, Hue (1892, p. 114); South India, Manalur, coll.: Foreau; Moreau (1952, p. 142).

It is likely that some of the earlier reports may now have to be transferred under *Ph. aspera* as the two are very much similar and the species name *Ph. aspera* did not exist then.

Physcia picta (Sw.) Nyl. var. ***endochroma.*** H. Magn. *et* Awasthi var. nov. A typo different thallus pallidus vel albo-pallidus, soredia intermedius subgranulosus et farinosus, medulla pallidoluteus, hypothecium K + rubescens.

Thallus up to 8 cm. in size, foliose, adpressed, plicate rugose longitudinally, laciniæ discrete only in the peripheral part. Thallus above

greyish-pale to glaucous-pale, scarcely pruinose in the peripheral lobes, sorediate; soralia globose, up to 1 mm. in size, distinct or crowded to confluent; soredia intermediate in nature between subgranular and white farinose; lower side black. Thallus up to 300 μ thick; upper cortex 20 μ thick; algal stratum 35–40 μ thick, medulla pale-yellow to colourless.

Thallus K + yellow, Cl −, K (Cl) −.

Apothecia numerous, crowded, superficial, sessile, 1–2 mm. in diameter; disc dark-brown, plane to ± concave by inflexed margin; margin thalline, entire to minutely sulcate. Thecium 80–90 μ thick, I + blue K −; hypothecium lenticular, 140 μ thick in the middle, dark-brown to brown-black in the upper part and brownish-red (K + red colouration) in the lower part. Asci 8-spored; spores brown, 2-celled, ellipsoid 15–18 × 5·5–7·5 μ in size, with acute ends, lumina minute, often transversely lentil-shaped (Text-Fig. 4), rarely 3-celled condition also observed. Paraphyses simple, 1·5 μ thick.

Habitat.—On bark of *Shorea robusta* tree.

Locality.—*E. Nepal,* Phenikhola valley, below Phidim, alt. 2,500 ft. D. D. Awasthi, 19-5-1953 (No. 2165 in Herb. *meo*)—TYPE.

Physcia picta var. ***isidiophora*** Nyl.

Reported from Calcutta, Nylander (1867, p. 7) and from Manalur, S. India, Moreau (1952, p. 142).

3. ***Physcia applanata*** (Fée) Zahlbr.

Reported as syn. *Physcia picta* var. *sorediata* from Manipur. Assam, Müll. Arg. (1892, p. 218).

4. ***Physcia aegiliata*** (Ach.) Nyl. (Plate I, Fig. 4).

In *Ann. Sci. nat., Bot., Ser.* 4, **15,** 1861, p. 43 A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 580—*Parmelia ægiliata* Ach. in *Method. Lich.*, 1803, p. 191.

Thallus foliose, suborbicular, adpressed, radiating, laciniate; laciniæ plane to somewhat convex and longitudinally plicate rugose to striate, centrally confluent densely covered by minute lobules and verrucæ and often almost subcrustaceous; laciniæ somewhat discrete only in the 5–10 mm. peripheral area, and then 1–1·5 mm. broad. Thallus above glaucous-white to glaucous-grey, smooth, somewhat waxy in appearance; underside black, scarcely black rhizinose or rhizinæ absent. No soredia and isidia.

Thallus 120–160 (200) μ thick in the lobes of the peripheral region, centrally thallus much thicker. Upper cortex 20–25 μ thick, paraplectenchymatous, cell lumina 3–4 μ in size; algal stratum continuous, 20–25 (35) μ thick; algal cells green roundish 8–12 μ in size; medulla colourless, hyphæ 3–4 μ thick, granular on the surface; lower cortex black 10–12 μ thick.

Upper cortex K + yellow; K (Cl) + yellowish; medulla K −, Cl−, I−, Pd−.

Apothecia in the central part of the thallus often crowded, and then irregular in outline due to lateral compression, otherwise round, sessile, usually 1 mm. (rarely up to 3 mm.) in diameter; disc plane to convex, black, epruinose; margin thalline, thick, entire to scarcely wavy crenate. Thecium 80–100 (120) μ thick, greyish in the upper part and colourless below, I+blue; K−; hypothecium dark-brown, lentiform or plano-convex (convex towards the thecium), 140–200 μ thick in the central part and gradually tapering to 5–10 μ to the margin, sharply demarcated from the medulla of the receptacle. Asci clavate, average 80 × 14 μ in size, with the 8 spores arranged biserially. Spores brown, 2-celled, thick-walled, oval ellipsoid, often more convex on one side, 16–20 × 6–8 μ in size, cell ends thickened more, lumina roundish to subangular, 3–4 μ in size (Text-Fig. 1). Paraphyses septate, conglutinate, clearing in K, simple, bifurcated and thickened apically to 3 μ.

Habitat.—On bark of trees.

Localities.—*Orissa*, Cheriakuda island, 1948, DDA (No. 310); *Andhra State*, Godavari district, Rampa Agency, alt. 3,500 ft., 1947, DDA (No. 140);

South India, Travancore, Quilon, 1953, O. A. Hϕeg (No. 2597);

Madurai, Shembaganur, G. Foreau, No. 56, 1957 (No. 3755);

Kodi, Rev. Fr. Leigh, 1906 (in herb. Magnusson—not seen by author).

E. Nepal, Biratnagar, alt. 1,000 ft., 1949, DDA and D. Chilkoti (No. 520).

The two specimens from South India (Nos. 2597 and 3755) which correspond to each other exhibit certain variations. The laciniæ are thicker and apothecia larger (up to 3 mm.). The medulla is at places orange-red to orange-brown in the lower part, which in K reacts to give a red colouration and thereby comes very near to f. *coccinea* Lynge.

Earlier Reports

From Nilgherries as syn. *Parmelia confluens*, Montagne (1842, p. 19); from Calcutta as syn. *Physcia confluens*, Stirton (1876, p. 188); from South India, Shembaganur, Kodaikanal and Manalur, coll. Foreau, Moreau (1952, p. 142) and from Nepal, downside of Kantonze bazar, alt. 1130 m., Asahina (1955, p. 63).

Sect. ***Euphyscia*** Th. Fr.; A. Zahlbr. in Engl. and Prantl *Pflazenfam.* 2 Auf. **Bd. 8,** 1926, p. 257

Characterised and distinguished from the other section by the colourless to pale colour of hypothecium. By far the majority of the species fall under this section.

5. ***Physcia endoxantha*** Strtn.

In *Transact. Philosoph. Soc. Glasgow*, **13.** 1881, p. 184 from Assam; A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 617.

6. ***Physcia detersa*** (Nyl.) Nyl. (Plate I, Fig. 8).

In *Flora*, **52,** 1869, p. 332; Poelt in *Mitteil. Bot. Staatssamml.* Monchen, H. **16,** 1957, p. 276—*Physcia pulverulenta* var. *detersa* Nyl. in Synops. Lich., **1,** 1860, p. 420—*Ph. grisea* var. *detersa* Lynge; A. Zahlbr., *Cat. Lich. Univ.*, **7,** 1931, p. 623.

Thallus foliose, suborbicular, to 3 cm. in size, adpressed; laciniæ crenate dissected, ± distinct throughout, somewhat concave above, to 1 mm. broad, ends narrower, rounded. Thallus above glaucous white to glaucous grey, densely white pruinose in the greater peripheral parts, centrally pale-grey to grey due to dense growth of the marginal soredia which gives a powdery appearance to this part; below pale-grey to brownish with dense, branched, brown-black rhizinæ.

Thallus 140–160 μ thick. Upper cortex paraplectenchymatous, 25–30 μ thick, with growth of pruina on the surface. Algal layer 20–25 μ thick, cells green, 12–14 μ in size. Medulla yellowish, hyphæ smooth, 3 μ thick, thin-walled. Lower cortex of longitudinally disposed hyphæ, 10–15 μ thick, brown-black. Rhizinæ to 100 μ thick at base.

Thallus K —, Cl —, Pd —, I—.

Specimens sterile.

Habitat.—On bark of trees.

Localities.—N.W. Himalayas, Kangra district, halfway Chhika to Manali, 1952, O. A. Hoeg (No. 1865 B), Kashmir, Gulmarg, alt. 9,000 ft., 1958, B. K. Kaul (No. 4000)—Agrees well with Poelt's exsiccatum 'Lichenes Alpium' No. 39. It forms a new report for India.

7. ***Physcia tribacea*** (Ach.) Nyl.

A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 693. Reported from Madura and Manalur, coll. Foreau, Moreau (1952, p. 142).

8. ***Physcia cæsia*** (Hoffm.) Hampe

A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 600. Reported under syn. *Parmelia caesia* Babington (1852, p. 249) from Kumaon, N.W. Himalyas.

9. ***Physcia endococcina*** (Körb.) Th. Fr.

In *Bot. Not.*, 1866, p. 150; A Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 615—*Parmelia endococcina* Körb. in *Parerga*, 1859, p. 36.

Thallus foliose, suborbicular, 2–3 cm. in size, adpressed, centrally almost subcrustaceous and peripherally minutely laciniate; lacinæ

up to 1 mm. broad and somewhat imbricated. Upper-side grey-brown to brown-black. smooth; lower side black, densely black rhizinose. No soredia and isidia.

Thallus 200–240 μ thick. Upper cortex paraplectenchymatous, 24–28 μ thick, cells thin-walled, lumina roundish to subangular $\pm$ honeycomb type, 6–10 $\times$ 5–8 μ in size. Algal stratum about 40 μ thick, algal cells green, 8–12 μ in size. Medulla reddish coccineus. hyphæ 4 μ thick. Lower cortex brown-black, 1–2 cell-layered, cell lumina varying from small to 15 μ in size.

Upper cortex K + yellow, Cl–, I–. Medulla K+purple-violet.

Apothecia superficial, sessile, roundish, up to 1·5 mm. in diameter; disc brown-black, smooth; margin thin, entire. Thecium 100–120 μ thick, reddish-brown in the uppermost region, I+blue, hypothecium yellow to orange. Asci club-shaped 80 $\times$ 25 μ, 8–spored; spores brown, 2-celled, ellipsoid, thick-walled, 20–26 $\times$ 9–13 (15) μ in size, cell lumen 6–8 μ in size (Text-Fig. 7). Paraphyses conglutinate, 1·5 μ thick.

Habitat.—Over ground, decaying basal parts of grasses or on bark.

Localities.—N.W. Himalayas, Almora district, alt. 4,500 ft., 1950, DDA and A. M. Awasthi (No. 591 B); Almora district, Phurkia near Pindari Glacier alt. 11,000 ft., 1950, DDA and A. M. Awasthi (No. 757); Dehra Dun, 1953, T. R. Seshadri No. A58, (No. 3726).

Physcia endococcina var. ***latiloba*** H. Magn.

apud Awasthi in *Proc. Indian Acad. Sci.*, **45 B,** 1957, p. 134.

A complete description of the variety is provided in the above reference. The localities other than those mentioned therein from where this variety has subsequently been collected are the following:

Kashmir near Pine view Hotel, T. R. Seshadri (No. A6, 1954) (No. 3401); *N.W. Himalayas*, Almora district, 1955, DDA (No. 3305), Jageswar, alt. 6,500 ft., 1956, DDA (No. 3507) and Mussoorie, alt. 6,500 ft., 1957, DDA (No. 3792). Almora district, 1958, DDA (No.3971). The spores (Text-Fig. 9) show greater resemblance to *Ph. setosa* rather than *Ph. endococcina.*

10. ***Physcia pulverulenta*** (Schreb.) Hampe.

apud Fürnr. in *Naturl. Topogr. Regensberg*, **2,** 1839, p. 249; A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 668—*Lichen pulverulentus* Schreb. in *Spicil. Flor. Lipsiens.*, 1771, p. 128.

Earlier Reports

From Himalayas in the region of Everest, Pauls (1925, p. 191); from Nepal, Asahina (1955, p. 63).

Physcia pulverulenta var. ***argyphæa*** (Ach.) Nyl.

In *Lich. Scandin.*, 1861, p. 109; A Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 677—*Parmelia pulverulenta* var. *argyphaea* Ach. in *Lichenogr. Univers.*, 1810, p. 474.

Thallus foliose, suborbicular, adpressed, stellate, contiguous, multifid, up to 5 cm. in size, laciniate; laciniæ obtuse, incised, crenate, partly plicate rugose, somewhat imbricated, up to 2 mm. broad. Thallus above ash-grey to brownish-grey, densely white pruinose; lower side black rhizinose; rhizinæ long, stiff and branched. No soredia and isidia.

Thallus 300–400 μ thick, paraplectenchymatously corticated on both the sides. Upper cortex (25) 40–60 (80) μ thick, the pruinose outgrowths about 20 μ thick, cell lumina 6–12 μ in size with 2 μ thick walls, inner outline of cortex irregular due to algal groups. Algal stratum discontinuous, cells in groups of 40 μ thickness; often algal cells dispersed deep within the medulla; algal cells (8) 12–16 μ in size, green. Medulla white, hyphæ semivertically disposed in the upper half part and $\pm$ longitudinally disposed in the lower half. Lower cortex dark-brown to brown-black, 25–30 μ thick.

Thallus K—, Cl—, K (Cl)—, Pd—.

Apothecia numerous, superficial, in the central part of the thallus, often crowded, sessile, $\pm$ rounded, mature ones 2–3 mm. in diameter; disc bluish-brown to ashy-brown, white pruinose, almost closed in the young stages, concave to plane later; margin thick ($\pm$200 μ), crenate to scantily proliferous, often inflexed, densely pruinose; pruina more prominent in younger stages. Thecium 160–180 μ thick, uppermost 20 μ brownish, colourless inwards, I + blue; hypothecium pale-yellow, 60 μ thick. Asci club-shaped 120–130 × 20–25 μ in size, 8-spored; spores brown to dark-brown (colourless when young), 2-celled, oval ellipsoid, narrower near the septum, 22–36 × 15–18 (20) μ in size, rather characteristic; cell lumina large roundish, wall uniformly 1·5–2 μ thick all round (Text-Fig. 11). Paraphyses conglutinated, 1·5–2 μ thick, branched at the apical parts and slightly thickened at the tips.
Habitat.—On bark of trees.

Localities.—Kashmir; Achhabal, alt. 6,500 ft., 1949, H. C. Raghubir (No. 544); Gulmarg range, Yarikale, alt. 7,000 ft., 1951, L. D. Kapoor (No. 992); Gulmarg, 1954, R. N. Chopra (No. 2608); Srinagar, 1953, DDA (No. 2618); Pahalgaon, alt. 7,000 ft., 1953, DDA (No. 2626); Baramula, 1954, T. R. Seshadri, No. F and A2, (Nos. 3410 and 3414).

11. ***Physcia askotensis*** Awasthi

In *Proc. Indian Acad. Sci.*, **45 B,** 1957, p. 131.

A complete description of the type specimen is provided therein. The species has since been collected from other localities noted below and exhibits the following variations:—

The laciniæ of thallus (in No. 3486) are narrower (less than 5 mm.). much discrete, deeply incised and untubercled in the central part. The apothecia (in Nos. 3484, 3521) are uniformly about 1 mm. in diameter with an olive-brown to dark-brown disc, which is ultimately

epruinose, the margin is very thin to almost superficially excluded in mature cases. It is noteworthy that in the type specimens the disc retains the pruinose nature with a thick margin. However, there is no dissimilarity in other characters and therefore I am inclined to consider these (at least for the present) as only ecological variants.

Localities other than Type

N.W. Himalayas, Almora and environs, alt. 5,500 ft., 1956, DDA (Nos. 3483, 3484, 3485, 3486—on *Aesculus indica* trunk; 3521 on conifer tree trunk); Mussoorie, alt. 6,500, 1957, DDA (No. 3793).

12. ***Physcia muscigena*** (Ach.) Nyl. (Plate I, Fig. 7).

In *Acta Soc. Linn. Bordeaux* **21,** 1856, p. 308; A Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 648—*Parmelia muscigena* Ach. in *Lichenogr. Univers.*, 1810, p. 472.

Thallus foliose, ascendent in the central parts, often growing to 6–8 cm. patches, laciniate lobate; laciniæ irregularly divided, rounded, densely imbricated, 1–1·5 mm. (up to 3 mm. at periphery) broad, somewhat concave on the upperside; laciniæ in the central part of thallus often with minute densely imbricated lobules. Thallus above bluish-grey to dirty-grey, densely white pruinose; lower side pale-brown, rhizinose; rhizinæ densely branched and attaching the thallus to the moss plants and other substrata. No soredia and isidia.

Laciniæ of the peripheral region 200–250 μ thick. Upper cortex 25–30 μ thick, paraplectenchymatous, cell lumina 8–10 μ in size, uppermost 8–10 μ region yellowish-brown and $\pm$ amorphous; externally irregularly granular with crystalline structures and hyphal projections which form the pruina on the surface. Algal stratum somewhat discontinuous, in the form of algal groups; algal cells large, rounded, 16–20 (24) μ in size. Medulla colourless (white) to scarcely pale; hyphæ smooth, 3–4 μ thick, thick-walled, lumen 1·5–2 μ. Lower cortex thin, pale-brown to brown, of compact longitudinal to sub-erect hyphæ; rhizinæ thick, 0·15 mm. at base, dark-brown to brown-black and densely branched.

Thallus K—, I—, Cl—, K (Cl)—, Pd—.

Specimens sterile.

Habitat.—On sloping ground among mosses in subshady places.

Localities.—N.W. Himalayas, Narkanda and Chini, Dr. Skoliezka No. 541 and no. nil respectively (in Hb. Cal.).

Kashmir, Srinagar, Shankaracharya hill, alt. 5,500 ft., 1953, DDA (No. 2639).

Earlier Reports

From Kumaon, N.W. Himalayas as syn. *Parmelia pulverulenta* var. *muscigena*, Babington (1852, p. 249).

13. ***Physcia sikkimensis*** Jatta

In *Bullet. del'Orto. Botan. Univers. Napoli*, **3**, 1911, p. 311; A. Zahlbr., *Catal. Lich. Univ.*, **7**, 1931, p. 681 from Sikkim.

14. ***Physcia rubricosa*** Strtn.

In *Proc. Philosoph. Soc. Glasgow*, **11**, 1879, p. 310, from Nilgherries; A Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 679.

15. ***Physcia hispida*** (Schreb.) Frege.

A. Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 626. Reported from Sikkim, Smith (1931, p. 132) and Chopra (1934, p. 74).

16. ***Physcia melanotricha*** Awasthi

In *Proc. Indian Acad. Sci.*, **45 B**, 1957, p. 133, from E. Nepal—a complete description is provided therein.

17. ***Physcia setosa*** (Ach.) Nyl. (Plate I, Figs. 5 and 6).

In *Synops. Meth. Lich.*, **1**, 1860, p. 429; A Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 679—*Parmelia setosa* Ach. in *Synop. Lich.*, 1814, p. 203.

Thallus foliose, often many thalli growing together and thus imbricating each other, individual thalli 6–8 cm. in size, suborbicular, laciniate; laciniæ subdichotomous to multifid, imbricated or superposing the older ones, plane to somewhat concave semi-canaliculate longitudinally. Thallus above ashy-white, glaucous-grey to darker grey, smooth; lower side black, densely rhizinose; rhizinæ much variable in length, black, throughout the underside and right up to the margin and often protruding beyond the thallus lobes at the periphery as cilia-like outgrowths. No soredia and isidia.

Thallus paraplectenchymatously corticated on both the sides. Upper cortex 25–35 μ thick, cell lumina 4–6 μ in size roundish to subrectangular. Algal stratum continuous, 30–40 μ thick; algal cells green, 12–14 μ in size. Medulla colourless, hyphæ smooth, 3–4 μ thick. Lower cortex 12–15 μ thick.

Thallus K—, Cl—, K (Cl)—, Pd—.

Apothecia usually present, superficial, sessile, with black cilia at the base, round when young, irregular in outline later, up to 3 mm. in diameter; disc dark-brown to brown-black, nude, plane to reflexed; margin thick entire, later somewhat crenulate. Thecium 90–110 μ thick, brownish in the uppermost 15–20 μ region, colourless inwards, I+ blue; hypothecium light yellowish, 15–20 μ thick. Asci clavate, 8-spored; spores brown, 2-celled, ellipsoid to oval ellipsoid (16) 20–30 $\times$ 10–12 (15) μ in size, thick-walled, lumen about 6 μ in size, roundish to transversely elongated (Text-Fig. 10). Paraphyses slender, apically shortly bifurcated and slightly thickened at the tips.

Habitat.—On ground, over stones and on bark of trees.

Localities.—N.W. Himalayas, Almora district, alt. 6,000–8,000 ft., 1950, DDA and A. M. Awasthi (Nos. 557, 677, 695 and 703); Almora district, Askote, alt. 4,500 ft., 1954, DDA (No. 2701); 1955, DDA (No. 3288); Almora, 1956, DDA (Nos. 3468, 3451 and 3526), 1958, DDA (Nos. 3964, 3983, 3989); Chakrata, alt. 7,500 ft., 1949, DDA, (No. 470); Tehri Garhwal, near Gangrani, alt. 7,000 ft., 1951, DDA (Nos. 890 and 966); Mussoorie, 1952, O. A. Hϕeg (Nos. 1438, 1448, 1452 and 3392); Mussoorie, 1957, DDA (Nos. 3790, 3791); Simla near Sanjauli, alt. 7,200 ft., 1952, DDA (No. 1428); Kangra district, Kulu, alt. 4,500 ft., 1952, O. A. Hϕeg (Nos. 1458, 1874); Dehra Dun and Mussoorie, P. N. Mehra, Nos. 32, 33 and 50 (in Hb. Magnusson); Narkanda, Dr. Skoliezka, No. 329 (Hb. Cal.); Mussoorie, alt. 7,000 ft., Amar Singh 14–3–1901 as No. 694, in Herb. E. Levier, det. Dr. Jatta (Hb. Cal.).

South India, Kodaikanal, alt. 7,000 ft., 1953, O. A. Hϕeg (No. 2532). *E. Nepal*, Mewakhola valley, alt. 11–12,000 ft., 1953, DDA (No. 2326).

In the majority of the specimens referred above, the width of the laciniæ was found to be 2–3 mm.; the laciniæ are contiguous from centre to periphery of the thallus; the rhizinæ are also 2–3 mm. long and protruded beyond the apex of the laciniæ. In specimen Nos. 677, 695 and 703 the laciniæ are much imbricated, narrower (1 mm. wide) and multifid; the rhizinæ are 1–1·5 mm. long and very dense. In 2326 the thallus is ashy-white, laciniæ much more divided and width being less than 0·5 mm., but the rhizinæ are longer (2–3 mm. long) and entangled with the mosses. Specimen No. 2701 exhibits certain sorediate protuberances along the margins of the laciniæ. Nos. 3288 and 3989 have small lobules developed later along the margin of apothecium and can be entitled to the status of an independent variety. Thus there is great variation in the habitat, habit and size of laciniæ and the apothecial character.

Earlier Reports

From Himalayas, Nylander (1860, p. 429); Hue (1892, p. 113); and Smith (1931, p. 132); from Nepal coll. Wallich as syn. *Parmelia atrocapilla*, Taylor (1847, p. 162).

Physcia setosa var. ***endococcinea*** Müll. Arg.

In *Journ. Linn. Soc. Lond. Bot.*, **29**, 1892, p. 218 from Manipur, Assam, coll.: G. Watt.; A Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 681.

18. ***Physcia albonigra*** (Schl.) Dalla Torre *et* Sarnth;

A. Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 599—from Himalayas in the region of Everest as syn. *Physcia melops*, Pauls (1925, p. 191).

19. ***Physcia integrata*** Nyl. (Plate I, Fig. 2).

In *Synops. Meth. Lich.*, 1860, p. 424; A. Zahlbr. in *Catal. Lich. Univ.*, **7**, 1931, p. 636.

Thallus foliose, suborbicular, adpressed, up to 5 cm. in size, often many thalli growing together, laciniate; laciniæ incised divided, confluent in the central part and discrete only in the peripheral region, plane to somewhat convex, 0·5–0·75 mm. broad, ± apiculate at the tip. Thallus above glaucous-white, smooth; lower side black, shortly rhizinose. No soredia and isidia.

Thallus 125–160 μ in thickness. Upper cortex 20–25 μ thick, paraplectenchymatous of 2–3 rows of cells, cell lumina in the exterior layer small (2–3 μ in size) and inner layer (8–10μ). Algal stratum dis; continuous, cells 10–12 μ in size, green, in groups. Medulla white-hyphæ 3 μ thick, superficially granular. Lower cortex dark-brown to brown-black, 12–15 μ thick, paraplectenchymatous.

Thallus K + yellow, Cl—, Pd—.

Apothecia superficial, sessile, round, to 1·5 mm. (rarely 2 mm.) in size; disc plane, dark-brown to brown-black; margin thin thalline, entire. Thecium 120–140 μ thick, yellowish-brown in the uppermost region, I+ blue; hypothecium pale to darkish-pale. Asci 100×25 μ in size, club-shaped, 8-spored; spores brown, 2-celled (rarely 1-celled also observed), ellipsoid, thick-walled, often with a slight constriction at the septum, 22–28×9–12 μ in size (Text-Fig. 8). Paraphyses slender, unbranched, tip yellowish-brown and thickened to 3 μ.

Habitat.—On bark of trees.

Locality.—South India, Madurai, Shembaganur, 1957, G. Foreau S. J. (No. 3745).

Earlier Reports of Varieties and Forma

Physcia integrata var. *sorediosa* Vain. from Kodaikanal, S. India, coll. Foreau, Moreau (1952, p. 142).

Ph. integrata var. *obsessa* Vain. from Kodaikanal, coll. Foreau, Moreau (*l.c.*).

Ph. integrata var. *obsessa* f. *hypoleuca* from Kodaikanal, Moreau (*l.c.*).

20. ***Physcia aipolia*** (Ehrht.) Hampe (Plate I, Fig. 9); apud Fürnr. in *Naturh. Topogr. Regensburg*, **2**, 1839, p. 249; A. Zahlbr. in *Catal. Lich. Univ.*, 7 1931, p. 590—*Lichen aipolius* Ehrht. apud Humb. in *Flor. Friburg. Spec.*, 1793, p. 19.

Thallus foliose, suborbicular, adpressed, radiating, to 5 cm. in size; laciniæ subdichotomously divided and imbricated, much reticulated in the central part of the thallus and smooth rounded and convex at the periphery and then 1–1·5 mm. broad. Thallus above glaucous-white to greyish-white, white maculate; maculæ sparse in the peripheral

lobes but dense and ± convex in the central part; underside pale-grey with grey rhizinæ. No marginal and apical cilia and no soredia and isidia.

Thickness of laciniæ, in peripheral part 250–300 μ. Upper cortex paraplectenchymatous, irregular in outline on the inner side, thickness varying from 15–40 μ, with an uppermost 10–12 μ region yellowish and rest colourless; cell lumina rounded to subangular and elongated vertically, 4–6 μ in size and moderately thick-walled; in horizontal section of the thallus, the lumen of the cells in the cortex about 4 μ in size with 2·5–3 μ thick amorphous walls. Algal stratum invariably discontinuous, 40–60 μ thick, algal cells green, 12–16 μ in size. The white maculæ seen on the surface of the thallus correspond to the areas devoid of algal cells inside the thallus and thus the discontinuous algal sratum is reflected on the surface by maculated areas. Medulla colourless (white); hyphæ superficially granular and 4 μ thick. Lower cortex of longitudinal to semi-vertical compact hyphæ with an outermost yellowish layer.

Upper cortex K+ yellow, Cl—, I—; Medulla K + faintly yellow or —, Cl—, Pd—.

Apothecia in the central part of the thallus, numerous, crowded, superficial, sessile, rounded to irregular in outline, 1–2 mm. in diameter; disc plane, white pruinose to ultimately epruinose, brown-black; margin thick, thalline, entire to inflexed crenulate in overmature ones. Thecium 90–110 μ thick, brownish in the uppermost 12–16 μ region and colourless inwards, I + blue; hypothecium colourless to faintly pale-yellow, 60–80 μ thick, uniform up to the margin; dispersed groups of algal cells present below the hypothecium. Asci club-shaped, 80 × 20–24 (32) μ in size, 8-spored; spores brown, 2-celled, ellipsoid, somewhat more convex on one side, thick-walled, 20–26 × 8–12 μ in size; lumen of cells with a bluish tinge, about 6 μ in size (Text-Fig. 5). Paraphyses conglutinated, 2 μ thick, sparsely bifurcated at the apical ends, somewhat thickened and yellow-brown at the tips.

Habitat.—On bark of trees.

Localities.—*N.W. Himalayas*, Kangra district, between Chikka and Manali, alt. 6,000–7,000 ft., 1952, O. A. Hφeg (No. 1863); *Kashmir*, Achhabal, alt. 6,500 ft., H. C. Raghubir, 1949 (No. 544 B); Gulmarg range, Yarikale, 1951, L. D. Kapoor (No. 992 B) and Pahalgaon, alt. 7,000 ft., 1953, DDA (No. 2622).

Earlier Reports

From Nilgherries as syn. *Parmelia stellaris* var. *aipolia*, Montagne (1842, p. 19).

21. ***Physcia alba*** (Fée) Lynge var. ***obsessa*** (Mont.) Lynge.

Specimen in Hb. Magnusson (*vide* his letter) from S. India, Kodi. coll. Rev. Fr. Leigh, 1906.

22. ***Physcia stellaris*** (L.) Nyl. (Plate I, Figs. 10 and 11).

In *Acta Soc. Linn. Bordeaux*, **21,** 1856, p. 307; A. Zahlbr. in *Catal. Lich. Univ.*, **7,** 1931, p. 681—*Lichen stellaris* Linn. in *Spec. Plant.*, 1753, p. 1144.

Thallus foliose, orbicular to suborbicular, stellate, adpressed, to about 2 cm. in size; laciniæ contiguous, incised, crenate, 0·5–1 mm. broad, marginally imbricated, convex on the upper side. Thallus above ashy-white to ashy-grey, smooth, without maculæ, epruinose and without cilia along the margins; lower side pale-yellow to pale-grey, rhizinose; rhizinæ grey.

Thallus 200 μ thick. Upper cortex 20–25 μ thick, paraplectenchymatous, cell lumina rounded to honeycomb type, 6–8 μ in size, thin-walled. Algal stratum 35–40 μ thick, continuous; algal cells green, 10–14 μ in size. Medulla colourless of loosely disposed 4 μ thick hyphæ. Lower cortex of compact longitudinally disposed hyphæ.

Thallus K + yellow, Cl—, K (Cl)—, Pd—.

Apothecia superficial, subsessile, rounded, up to 1·5 mm. in diameter; disc bluish to brown-black, white pruinose; margin thin, entire. Thecium 100–120 μ thick, brownish in the uppermost about 10 μ region, colourless inwards, I + blue; hypothecium colourless to light-pale. Asci clavate 85 × 16–20 μ in size, 8-spored, arranged biserially; spores dark-brown to brown-black, 2-celled, ellipsoid 16–20 (22) × 8–11 μ in size; cell lumen 6–8 μ, roundish or with a concavity towards the ends (Text-Fig. 12). Paraphyses 1·5 μ thick, apically bifurcated and thickened to 3 μ at the tip.

Habitat.—On tree trunks.

Localities.— *N.W. Himalayas*, Pangi, Dr. Skoliezka, No. 459 (Hb. Cal.); Kashmir, Pahalgaon, alt. 7,000 ft., 1953, DDA (2625) and 1954, R. N. Chopra (No. 2609).

In specimen No. 2625 the growth of the thallus is somewhat unilateral, the laciniæ are narrower (0·5 mm. broad) discretely apart, the rhizinæ short, brownish and along the margins only and thus *cf.* var. *tenera* (Havaas) Lynge. The specimen No. 2609 has the laciniæ 0·5–1 mm. broad and are stellate radiate and thus *cf.* var. *radiata* (Ach.) Nyl.

Earlier Report

From Kumaon, N.W. Himalayas, as syn. *Parmelia stellaris*, Babington (1852, p. 249).

SUMMARY

1. The paper deals with the species of the genus *Physcia* from India and Nepal. The study is primarily based on the lichen specimens preserved in the author's private herbarium.

2. Keys as an aid to the identification of the 22 species of *Physcia* known so far from this region have been drawn out and 13 species have been worked out in detail.

3. The varieties designated as new are *Ph. aspera* var. *alutacea* H. Magn. *Ph. picta* var. *endochroma* H. Magn. *et* Awasthi.

4. The species being reported for the first time from this area are: *Physcia aspera* H. Magn.; *Ph. detersa* (Nyl.) Nyl. and *Ph. endococcina* (Körb.) Th. Fr.

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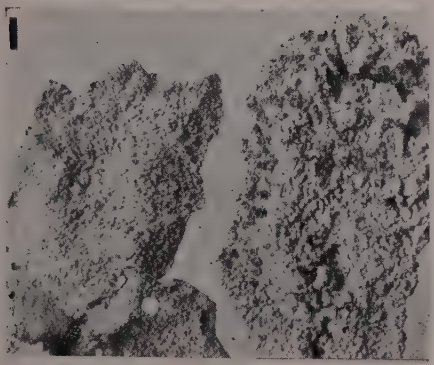

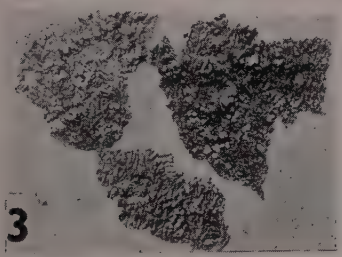

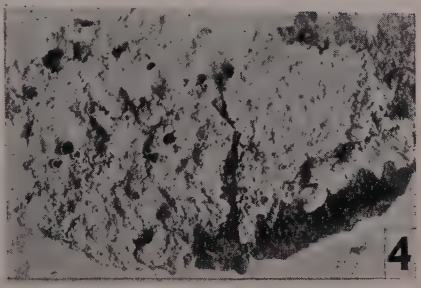

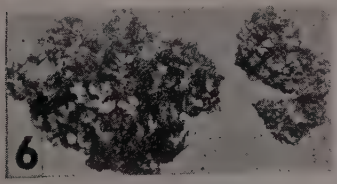

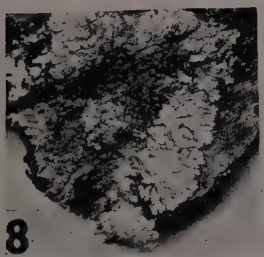

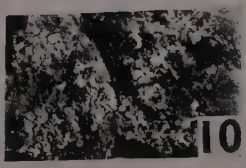

D. D. Awasthi

Explanation of Plate I

Fig. 1. *Physcia aspera* H. Magn. (No. 3381), ×9/10.
Fig. 2. *Ph. integrata* Nyl. (No. 3745), ×9/10.
Fig. 3. *Ph. picta* (Sw.) Nyl. (G. Panigrahi No. 5400), ×9/10.
Fig. 4. *Ph. aegiliata* (Ach.) Nyl. (No. 2597), ×1.
Fig. 5. *Ph. setosa* (Ach.) Nyl. (No. 3468), ×6/10.
Fig. 6. *Ph. setosa* (Ach.) Nyl. (No. 677), ×9/10.
Fig. 7. *Ph. muscigena* (Ach.) Nyl. (No. 2639), ×9/10.
Fig. 8. *Ph. detersa* (Nyl.) Nyl. (No. 4000), ×9/10.
Fig. 9. *Ph. aipolia* (Ehrht.) Hampe. (No. 544B), ×12/10.
Fig. 10. *Ph. stellaris* (L.) Nyl. (No. 2625), ×9/10.
Fig. 11. *Ph. stellaris* (L.) Nyl. (No. 996), ×9/10.

SUCCESSION IN SOME *SHOREA ROBUSTA* FORESTS OF U.P.

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(Received for publication on April 23, 1959)

Information on succession provides the necessary knowledge regarding the rate and manner in which the composition and structure of existing stand is being, or may be, altered by natural processes. Every plant community is thus governed by natural and dynamic tendencies, acting either to progress it towards higher life-forms or to retrograde it towards lower stages. Sometimes this change is temporarily arrested to form a stable stage in the process of succession.

The climax is reached only after a very long period of continuous adjustment which may sometimes be reckoned in terms of geological ages. It is a well-known fact that most of the present-day species evolved in later geological epochs are still migrating and have not attained the maximum limit of distribution on all suitable soils and in all congenial climatic regions. Necessarily, therefore, they have not yet attained enough stability in such areas to form the climax vegetation. This picture is furthur complicated by the operation of many limiting conditions, chiefly biotic and edaphic, which impose a cyclical pattern of progression and retrogression, both primary and secondary, on plant communities, resulting not only in changes in their floristic organisation but also in their limits of distribution which shrink and expand in conformity with distributing influences. Sal forests are no exception to this rule and under the shifting emphasis of different environmental factors they are undergoing a slow change in range distribution and composition. The natural process on succession, if undisturbed, attains its climax only after the lapse of a very large number of plant generations.

Therefore, a precise knowledge of these natural and dynamic tendencies, together with the stage to which a particular plant community can be assigned, immensely helps in the management of that community to attain desired objectives by suitably guiding the natural processes of change and adjustment.

The Sal (*Shorea robusta*) forests of Uttar Pradesh are distinguishable into two broad types, *viz.*, Dry sal forests (including sub-types A_1 and A_2) and moist sal forests (including sub-types B_3 and B_4). These may be regarded as variants of a climatically conditioned *Shorea robusta* community occurring on well drained fairly deep, usually loamy and adequately moist type of soils, and largely protected from hazarduous effects of biotic influences. *Shorea robusta* regenerates to a certain

extent but the reproduction does not cover extensive areas. It occurs as patches in the general type of dry and moist *Shorea robusta* forests, wherever the growth conditions are most favourable.

The dry type of sal forest is mainly confined to dry Siwalik or alluvial soils, and is heavily subjected to biotic influences. It is, thus, a retrogressed stage of fairly stable nature, in which *Shorea robusta* does not, on the whole, regenerate naturally. Severity of grazing and fires, no doubt, further degrade this type but this change is comparatively slow. If protection is afforded there on suitably moist and deep soils it progresses towards the normal moist type, in which natural regeneration of *Shorea robusta* is in fair abundance. This change towards the progressive side occurs in short successive stages but there is no clear differentiation of the various seral stages. On poor soils it is perhaps a climax, at the extreme end of the dry deciduous mixed forest. On such soils it may degrade to mixed forest without *Shorea robusta*. It, therefore, forms a sort of tension zone, which is flanked on one side by the moist *Shorea robusta* association and on the other side either by dry mixed deciduous forest (without *Shorea robusta*) or a very dry *Shorea robusta* forest of xerophytic nature.

The xerophytic stage of the dry *Shorea robusta* forests is mainly dominated by tree species like *Anogeissus latifolia*, *Acacia catechu* and *Aegle marmelos*. The grass *Eulaliopsis binata* is, by far, the commonest. Ultimate degradation of this stage results into dry type of short grass savannah. The normal type of dry *Shorea robusta* forest, conditioned by biotic factors, is characterised by species like *Diospyros tomentosa*, *Holarrhena antidysenterica*, *Aegle marmelos*, and *Anogeissus latifolia*.

The lower limit of moist *Shorea robusta*, where it merges with the dry *Shorea robusta* type, is typified by an annual rainfall of 1143 mm. Annual precipitation of 1270–1524 mm. represents conditions most favourable to the growth of *Shorea robusta*, in which it regenerates freely. Further increase in rainfall induces the preponderance of an evergreen type of shrubby layer which inhibits the natural regeneration of *Shorea robusta*. It is, therefore, the effective precipitation of about 1397 mm. which controls the existence of normal type of moist *Shorea robusta* forest. Even in the dry *Shorea robusta* type, localized patches may receive more soil moisture due to certain physiographic features, proximity to watercourses, protection from grazing and fires, or due to certain structural and textural properties of soil. This results in the occurrence of moist *Shorea robusta* oases in the general dry *Shorea robusta* type. Similarly in areas subjected to heavy rainfall, optimum soil moisture conditions may arise owing to certain topographical features, slope of terrain, controlled grazing and fires and soil properties leading to excessive underground drainage.

Due to the intermediate position occupied by the moist type of *Shorea robusta* forest, as explained above, retrogression, if it sets in under biotic or bio-edaphic influences, followed varied courses. In a habitat with low effective soil moisture, or low water-table, it quickly retrogresses to dry *Shorea robusta* type and continued effects of adverse factors

degrade it finally to a short grass savannah, as in the case of ordinary dry *Shorea robusta* type.

In localities where effective soil moisture is higher, or where the water-table is high, retrogression finally results in a tall-grass savannah, passing through an intermediary stage of moist miscellaneous forest with heavy grass. As a process of secondary succession, clear felling of trees in moist *Shorea robusta* forest also tends to uplift the water-table and grass communities of *Narenga porphyrocoma*, *Arundo donax* and *Phragmites maxima* arise and stabilise. As large stretches of this type of tall-grass savannah are in existence, probably it is correct to designate this stage as post-climax.

Primary Succession

In the case of dry *Shorea robusta* type, the primary succession also commences from a stage of grassland type, similar to the one into which a dry *Shorea robusta* type ultimately retrogrades, under continued biotic influences. The pioneer grasses are *Saccharum spontaneum*, *Erianthus munja*, *Neyraudia arundinacea*, etc. Further progression leads to open grassy savannah, then to open savannah miscellaneous forest and so on, until a good depth of loamy soil, capable of supporting sal (*Shorea robusta*), is built up. The occurrence of savannah forest in the zone of dry *Shorea robusta* type, therefore, represents a transitional seral community which may be maintained for unduly long periods, as a suitable sub-climax under continued effects of grazing and fires.

The grassy savannahs are gradually colonized by *Acacia catechu* and *Dalbergia sissoo*, which form a distinct stage in the developmental succession. This stage is followed by a mixed type of forest with species like *Holoptelia integrifolia*, *Dalbergia sissoo* and *Salmalia malabarica*. This forms a fairly stable community and may be regarded as a sub-climax on suitable soils. Further development of this stage leads the formation of dry type of *Shorea robusta* forest, and retrogression converts it to a dry savannah. It is, therefore, a critical stage in the succession of dry type of *Shorea robusta*. Under favourable conditions the mixed miscellaneous forest without *Shorea robusta* endures.

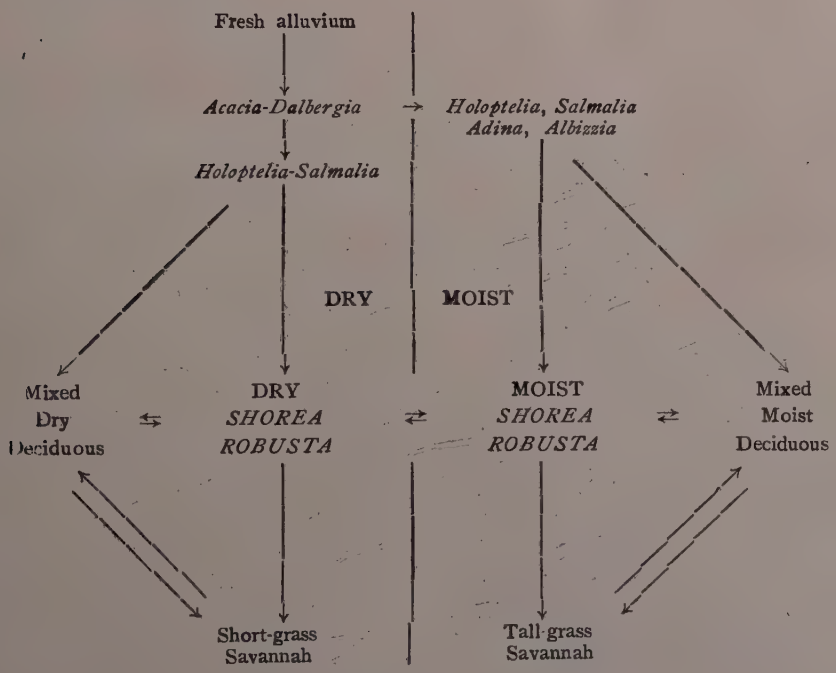
The possible sites, where primary succession leading to moist *Shorea robusta*, may commence, are riverain alluvial deposits and the Siwalik clays and conglomerates in the moisture zone. The riverain alluvial deposits have a brief initial grassy stage and are quickly colonized by tree species like *Acacia catechu*, *Dalbergia sissoo*, and *Zizyphus* spp. This stage lasts for a fairly long period and is then followed by a community of *Holoptelia integrifolia*, *Adina cordifolia*, *Albizzia procera*, *Salmalia malabarica*, *Stereospermum suaveolens*, *Butea monosperma*, *Albizzia lebbek*, and *Lagerstræmia parviflora*, etc. The ameliorative effect of this type of mixed forest results in the building up of a good depth of humified loamy soil which is more retentive of moisture for the survival and development of sal seedlings. *Shorea robusta* enters in, and in the next successional stage, a community of *Shorea robusta*, *Terminalia tomentosa*, and *Syzygium cumini* arises. It is a fairly stable stage and

may be regarded as a sub-climax. Further developmental stages are not known, but it is certain that under moderate influence of biotic factors it reverts to a drier *Shorea robusta* forest. On more moist soils, if the continuity of these factors persists, a moist savannah of tall-grass results.

On the Siwalik clays and conglomerates, the initial stage is a grass-land community which may linger on for a long period. It is followed by a community of *Salmalia malabarica*, *Albizzia procera*, *Cedrela toona* and *Trewia nudiflora*. And finally, *Shorea robusta* comes in with *Ougeinia dalbergioides* and *Syzygium cumini*, as the main associates.

From the above account, it is clear that, apart from the climatic influences, the development and existence of *Shorea robusta* forest is mainly controlled by edaphic and biotic factors. It is not very stable in nature and may be regarded as a predominantly bio-edaphic pre-climax association in the tracts under consideration.

The following is the diagrammatic representation of the various successional and retrogressive stages in these types of *Shorea robusta* forests in Uttar Pradesh.



SUMMARY

Succession studies in the dry and moist *Shorea robusta* types indicate that there is evidence for both the main lines of successional changes,

namely, progression and retrogression. The dry *Shorea robusta* types (A_1 and A_2) ultimately degrade into a grassy savannah of dry type passing through the mixed miscellaneous stages. The primary succession in the dry sal type starts from grassland association with species like *Saccharum spontaneum*, *Erianthus munja*, etc., which leads to the mixed miscellaneous stage. This may retrograde to deciduous forest or to mixed forest with *Shorea robusta* and finally to a dry savannah.

In the moist *Shorea robusta* type the primary succession starts from grasses and leads to mixed forests of *Shorea robusta* with *Terminalia tomentosa*, *Syzygium cumini*, etc., after passing through mixed miscellaneous seral stages. This moist *Shorea robusta* may degrade into dry *Shorea robusta* type than to mixed miscellaneous forests and ultimately to dry savannah. In localities with high water-table and under moist conditions, retrogression may proceed towards savannah with tall-grasses. The tall-grass savannah may be more or less stabilised as a sort of post-climax association.

Acknowledgements

I gratefully acknowledge my thanks to Sri. S. K. Seth, Head. Division of Forestry, Forest Research Institute and Sri. M. A. Waheed Khan. Ecologist, F.R.I., for suggestions and criticism.

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CYPERACEÆ FROM MOUNT ABU

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(Received for publication on June 8, 1959)

Mount Abu (24° 36′ N. and 72° 43′ E.) lies at the south-western extremity of the Aravalli Hills. It is about 1385 meters above sea-level and has been developed as a hill-station since long. The place has a pleasant climate with a rainfall of about 175 cm. which favours the growth of a luxuriant flora, which has, no doubt, attracted the attention of some of India's leading botanists.

The flora of Mt. Abu has been considerably explored by Sutaria (1941), Mahable and Kharadi (1942) and Raizada (1954). The authors of this note feel that the Family Cyperaceæ has not been fully dealt with and hence an attempt has been made in this note to present a complete list of Cyperaceous plants collected from Mt. Abu during the monsoons of 1957 and 1958. Brief notes on the habitat and localities of the plants have been given. This note aims at making the flora of Mt. Abu more comprehensive.

Out of the 23 species mentioned below, a few plants such as *Cyperus difformis*, *Pycreus sanguinolentus*, *Cyperus exaltatus*, *Stenophyllus capillaris*, *Eriophorum comosum*, and *Carex myosurus* have already been reported from this place by previous workers. The rest of them, as far as the authors are aware, are recorded for the first time from the area.

1. *Pycreus sanguinolentus* Nees.

An erect herb with dark-red spikelets on a simple umbel, in marshes-Polo ground; backside of the Bharatiya Lodge; on way to Nakhi Lake; Gaumukh.

2. *Pycreus pumilus* Turrill.

A small slender annual, spikelets yellow to golden-brown; in comparatively drier areas, Gaumukh.

3. *Juncellus lævigatus* C. B. Cl.

Plants with creeping rhizomes, spikelets in compact heads borne above the middle of the stem; rare, in marshes-Polo ground.

4. *Cyperus difformis* Linn.

Stems triquetrous, spikelets either green or golden-yellow; in marshes everywhere; fairly common on way to Gaumukh.

5. *Cyperus globosus*

(*Cyperus flavidus* Retz.)

Collected from a few places on way to Nakhi Lake.

6. *Cyperus leucocephalus* Retz.

Erect annuals with spikelets in white globose heads; under the shade of forest trees on way to Gaumukh.

7. *Cyperus aristatus* Rottb.

Small tufted annual, spikelets with recurved arista; on way to Nakhi Lake.

8. *Cyperus compressus* Linn.

Fairly common on Polo ground and on way to Nakhi Lake.

9. *Cyperus iria* Linn.

10. *Cyperus iria* var. *paniciformis* Clarke.

Both the type and variety are found at the Polo ground and on way to Sunset point.

11. *Cyperus corymbosus* Rottb.

A tall glabrous herb, spikelets brown; on the banks of streams on way to Mt. Abu from Abu road.

12. *Cyperus rotundus* Linn.

Found on the backside of the Bharatiya Lodge; on way to Gaumukh.

13. *Cyperus imbricatus Retz.**

(*Cyperus radiatus* Vahl.)

Reported by Sedgwick in his revision of the Cyperaceæ of the Bombay Presidency.

14. *Cyperus exaltatus* Retz.

A sturdy plant, spikelets chestnut-brown; abundantly found in a marsh-Polo ground.

15. *Cyperus paniceus* Boeck.

(*Mariscus paniceus* Vahl.)

Plants with slender stolons; a typical forest plant; on way to Sunset point and Gaumukh.

16. *Cyperus triceps* Endl.

(*Kyllinga triceps* Rottb.)

Plants of open grassland, heads pure white; backside of Bharatiya Lodge; on way to Nakhi Lake.

17. *Cyperus brevifolius* Hassk.
(*Kyllinga brevifolia* Rottb.)

Plants with slender creeping rhizomes, heads greenish near habitation on way to Abu road.

18. *Cyperus metzii* Mttf.
(*Kyllinga squamulata* Vahl.)

A tufted herb, heads greenish; along the roadside.

19. *Fimbristylis dichotoma* Vahl.

Densely tufted, spikelets in compound umbels; near habitation on the banks of ditches.

20. *Stenophyllus barbata* Rottb.
(*Bulbostylis barbata* Kunth.)

Small annuals found on light sandy soils; on way to Nakhi Lake.

21. *Stenophyllus capillaris* Rottb.*
(*Bulbostylis capillaris* Kunth.)

Reported by Raizada in his paper on a botanical visit to Mt. Abu.

22. *Eriophorum comosum* Wall.

A sturdy plant, spikelets in decompound umbels; scales pappus-like.

23. *Carex myosurus* Nees.*

Reported by Raizada[5] and Sutaria.[7]

Note.—The plants marked with an asterisk were not collected by the authors.

ACKNOWLEDGEMENT

We are indeed thankful to Shri M. B. Raizada, Officer-in-Charge, Botany Branch, Forest Research Institute, Dehra Dun, for the determinations of the plants and for his useful suggestions during the preparation of this note.

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SOME NEW PLANT RECORDS FOR NAGPUR

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(Received for publication on May 27, 1959)

Introduction

Nagpur is one of those regions in our country where there has not been practically any systematic botanical exploration. The partial lists prepared by Graham (1911, 1913) are the only authentic and relevant literature available on the flora of this place. In the works of Haines (1916) and Witt (1916) there are casual references to the plants of this area. There is no comprehensive flora for Nagpur and its neighbouring regions.

Further, even these records need a thorough revision in view of recent changes in the taxonomy and nomenclature of plants and also in the light of new findings about the occurrence, distribution and abundance of the various species. Also, during the last few decades several new species like *Acanthospermum hispidum* DC. and *Gomphrena celosioides* Mart. have entered this area and have become more or less naturalized.

Hewetson (1951) drew attention to this gap in our knowledge of the Indian flora and made a strong appeal for the preparation of a flora for (the old) Madhya Pradesh. Santapau (1956) rightly emphasised the need for investigating such, as yet little explored, regions of our country. The author (1954), during the course of his investigation of hydrophytes, listed a number of species of water and marsh plants, previously unrecorded from this place.

As a preliminary step towards the compilation of an up-to-date comprehensive flora of Nagpur, it is intended to record here the occurrence of certain species which have not been listed in the available literature cited above, with brief notes on their habitats and their important diagnostic characters.

Menispermaceæ

1. ***Stephania hernandifolia* (Willd.) Walp.**

So far seen only at the Starky Point; rare. *Flowers and Fruits*: August to October. *Mirashi*, 11.

Elatinaceæ

2. ***Bergia ammannioides* Roxb.**

Found on the northern shores of the Gorewara lake and in rice fields behind Maharajbag; abundant; very easily confused with the Ammannias. *Flowers and Fruits*: December to February. *Mirashi* 118.

COMPOSITÆ

3. ***Acanthospermum hispidum* DC.**

Annual, erect, biparous-cymosely branched herb; stems hairy; leaves opposite, hairy. Capitula solitary in the forks of branches, many flowered, heterogamous; ray florets uniseriate, female, ligulate; disc florets functionally male, tubular, with an abortive ovary and a style with a single papillose stigma. Cypselas spinous.

This comparatively recently introduced species is now spreading rapidly. It can be seen at several places along the Amravati Road, at Gorewara and at Koradi also. It is usually found in association with *Xanthium strumarium* Linn., *Tephrosia purpurea* Pers. and *Achyranthes aspera* Linn. Pure stands of the species are also occasionally met with. *Flowers and Fruits*: August to October. *Mirashi* 103.

PRIMULACEÆ

4. ***Anagallis arvensis* Linn.**

Found in agricultural fields; occasionally at other rather damp places. *Flowers and Fruits*: September to December. *Mirashi* 42.

It resembles somewhat *Exacum pedunculatum* Linn.; but, it can be easily distinguished by the long pedicels of the flowers and the rotate corolla.

CONVOLVULACEÆ

5. ***Operculina turpethum* (Linn.) Silva-Manso.**

On the hedges of the agricultural fields behind Maharajbag; so far seen only at this spot; very rare . *Flowers and Fruits*: September to January. *Mirashi* 110.

SCROPHULARIACEÆ

6. ***Kickxia ramosissima* (Wall.) Janchen**
Linaria ramosissima Wall.

Grows on walls and housetops, not common, scarce. *Flowers and Fruits*: August to September. *Mirashi* 147.

7. ***Sutera dissecta* (Del.) Walp.**
Sutera glandulosa Roth.

Grows in wet places; seen near Bhide Talao; fairly abundant. *Flowers and Fruits*: December to February. *Mirashi* 145.

8. ***Centranthera nepalensis* D.Don.**
Centranthera hispida Hook. f.

Found in agricultural fields and on the banks of the Nag River; not common, scarce. *Flowers and Fruits*: September to December. *Mirashi* 227.

The sparingly branched scabrid habit, the linear leaves and the rather large rosy flowers are quite characteristic.

LENTIBULARIACEÆ

9. ***Utricularia flexuosa*** **Vahl.**

This species grows luxuriantly in the waters of the Sakkardara Talao. The stolons are often few meters long. *Flowers and Fruits*: September to December. *Mirashi* 121.

ACANTHACEÆ

10. ***Hygrophila quadrivalvis*** **Nees**

This is one of the rarer species of India. At Nagpur it is extremely rare. It has been seen only at one spot—in the shallow bed of the Nag River near its source, forming pure stands. *Flowers and Fruits*: October to December. *Mirashi* 169.

The species is classed as "glabrous or so" by Haines (1922) although in the detailed note on the species, he describes it as "a rather coarse herb with strigillose or glabrescent stem and leaves which are hairy above". "Glabrate" is the word used for the leaves of this species by C. B. Clarke in Hooker, f. (*Fl. Brit. India*, **4**: 408). The word is not found in the original description of the species by Nees. From these descriptions, however, it appears that there are various forms of this plant. The Nagpur plants have profusely hairy stems as well as leaves which are hairy on both surfaces. This striking hairiness is in accordance with Nees's description.

The author is indebted to Father H. Santapau for this information about the species.

11. ***Ruellia tuberosa*** **Linn.**

An erect herb, about 30–35 cm. high, somewhat glabrous, with a number of tuberous roots; leaves opposite, elliptic-obovate. Flowers blue, large, handsome, in axillary and terminal cymes; bracteoles linear and shorter than the calyx; corolla subequally 5-lobed, lobes twisted to the left in the bud; pollen grains 3-porous. *Flowers and Fruits*: May to August. *Mirashi* 202.

This plant, introduced from America, now seems to be spreading in Nagpur. It is the only species of the genus in Nagpur. I have not seen it cultivated in gardens. It is seen growing in shady places in lawns. The attractive showy flowers commend it for being cultivated as an ornamental garden plant.

12. ***Gantelbua urens*** **(Heyne ex Roth) Brem.**

Hemigraphis dura T. Anders.

Common in the first half of the hot season; on waste land and on the edges of the field; not abundant. *Flowers and Fruits*: March to May. *Mirashi* 137.

The presence or absence of hairs on the upper parts of the filaments of the longer stamens is a somewhat variable character and therefore not a satisfactory criterion for distinguishing the species.

VERBENACEÆ

13. ***Stachytarpheta urticæfolia* (Salisb.) Sims.**

Stachytarpheta indica auct. (non *Verb. indica* Linn.)

Grows in cool shady, watery places near the Telankhedi Forest. Here the plants are very healthy; especially behind the Vanamahotsava Nursery these plants show a luxuriant growth; not seen at any other place. *Flowers and Fruits*: December to March. *Mirashi* 193.

This is another plant which should be cultivated in the garden along with the other usually cultivated species of this genus.

LABIATÆ

14. ***Nepeta hindustana* (Roth) Haines**

Nepeta ruderalis Buch-Ham.

Occurring profusely in the damp areas near the Bhide Talao; not common, abundant. *Flowers and Fruits*: December to February. *Mirashi* 148.

AMARANTACEÆ

15. ***Gomphrena celosioides* Mart.**

A much branched, perennial, prostrate herb with a long stout tap root; stem hairy; leaves opposite; Flowers greenish-white, in dense terminal or axillary spikes; bisexual; bracteoles 2; perianth members 5, woolly; staminal tube 5-fid, long, anthers yellow; ovary one-celled with one ovule, style short, stigma bilobed. Fruit enclosed in hardened, persistent perianth; seeds reddish-brown, shining.

A recently introduced herb, now fairly common in lawns. *Flowers and Fruits*: almost throughout the year. *Mirashi* 50.

16. ***Alternanthera paronychioides* St. Hil.**

A prostrate, hairy herb; stem cylindrical, red; leaves opposite, ovate; flowers white, in axillary clusters; perianth members 5, with long white hairs at the back, unequal; stamens 5, staminal tube short, anthers one-celled; ovary one-celled, ovule one, suspended from a basal stalk, stigma subsessile, papillose.

Grows in drying ditches and ponds along with *Polygonum plebeium* R. Br. and *Glinus lotoides* Linn.; not common, fairly abundant. *Flowers and Fruits*: October to April. *Mirashi* 218.

ORCHIDACEÆ

17. ***Eulophia campestris* Wall.**

Grows among grasses on the banks of the Nag River when water has receded; not seen elsewhere, rare. *Flowers and fruits*: March to April. *Mirashi* 30.

18. ***Zeuxine strateumatica* (Linn.) Schltr.**
Zeuxine sulcata Lindl.

Found on the banks of the Nag River along with *Eulophia campestris* Wall.; also found in the lawns of the College of Science; not found elsewhere; rare. *Flowers and Fruits*: March to April. *Mirashi* 29.

Liliaceæ

19. ***Scilla indica* Baker**

Found all along the Amravati Road near the Starky Point and also at Gorewara. *Mirashi* 31.

The plants appear immediately after the first monsoon shower in late June or early July. The flowering season is extremely short. By the end of August there is hardly any trace left of these plants.

Acknowledgment

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EMBRYOLOGY OF THE GENUS *PSIDIUM*

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The genus *Psidium* belonging to the family Myrtaceæ, probably represents a very ancient group of plants. *Psidium guajava* L., a native of tropical America, is almost naturalized in many parts of India and is chiefly cultivated for its fruits. In Assam, the leaves and barks of the plant are employed in dyeing and in Bengal and Uttar Pradesh, for tanning. The wood of *Psidium* is close-grained and takes on a beautiful polish.

Psidium cujavillus Brum. resembles *P. guajava* and is known more recently as another form of the latter (*Psidium cujavillus* Brum. f. Ind. 114 = *P. guajava* L., *Ref. Index Kewensis* Pt. II, 1946; p. 640). However, there is a marked difference in size of the leaves and fruits between the two species. The leaves of this plant are small and measure $1 \cdot 4'' \times 0 \cdot 5''$ while those of *P. guajava* are $5'' \times 2''$. The fruits are also smaller. *P. cujavillus* flowers twice a year, once in the month of April and then in the month of September under local climate.

Although several members of the family are well represented in the tropics and in European conservatories, their embryology have not been investigated extensively. Moreover, the family has an added interest in that some of the species show polyembryony (Tiwary, 1926; Pijl, 1934; Johnson, 1936). Investigations were, therefore, undertaken in order to explore the nature of embryo development and the extent of polyembryony if any, present in the genus *Psidium*.

Material and Methods

Materials of *Psidium guajava* L. were collected from an orchard in Allahabad and that of *P. cujavillus* Brum. from the botanical gardens of Banaras Hindu University, Varanasi, in the years 1952 and 1955 respectively by one of us (S. K. R.). Fixations were done between 9 and 11 a.m. in the fields in formalin-acetic-alcohol after trimming off the ovary wall so as to facilitate penetration of the fixing fluid. The customary procedures of infiltration and imbedding were followed. Sections were cut at 10–20 μ thick depending upon the stage of development. The slides were stained both in Haidenhain's iron-alum hæmatoxylin and a combination of safranin and fast green.

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Observations

Ovary and ovules.—The ovary is inferior and four to five-celled and contains an indefinite number of ovules borne on projecting axile placentæ. Embedded in the superficial layers of the thick ovary wall are numerous lysigenous oil glands. "Grit" cells and druses are also found scattered irregularly in the pericarp.

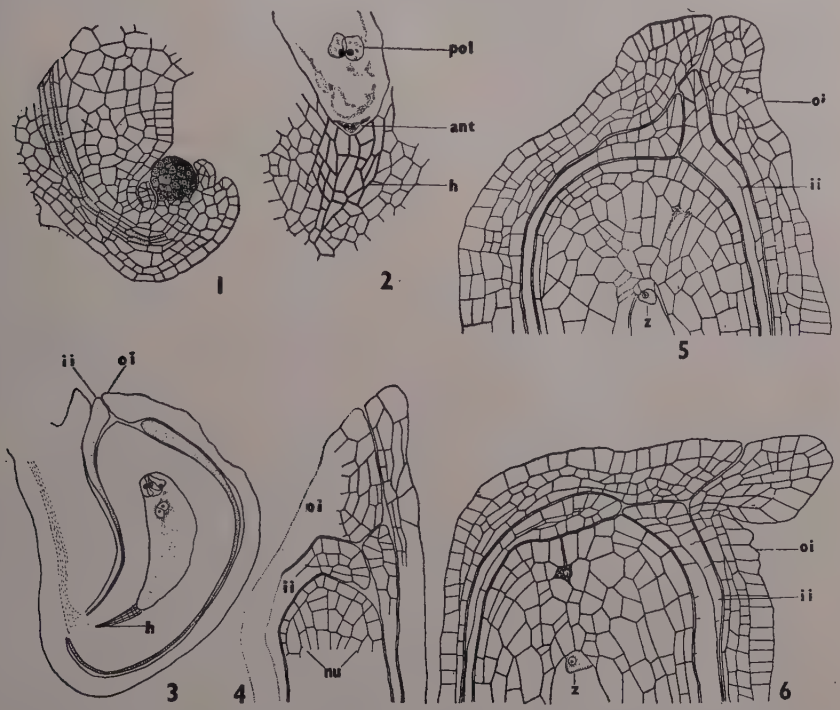
The ovules are anatropous and bitegminal with a conspicuous bend at the chalazal region towards the raphe (Text-Figs. 1, 3, 34). Owing to compression by mutual pressure of the large number of ovules some remain "hemi-anatropous" as in *Psidium cujavillus* (Text-Figs. 35, 36).

The ovule originates as a nucellar primordium which soon grows in size. The inner integument is differentiated first followed closely by the outer one when the ovule begins to curve (Text-Fig. 1). The two integuments overtop the nucellus and together form the micropyle which may be somewhat zig-zag (Text-Figs. 4–6, 35, 36). In *Psidium guajava* the inner integument does not cover the entire nucellus but stops short at some distance away from the summit of the nucellus. On the funicular side, however, it grows normally and together with the portion of the outer integument from the opposite side, forms the micropyle (Text-Fig. 3). Occasionally the inner integument alone forms the micropyle, as in *P. cujavillus* (Text-Fig. 37). Of the two integuments the inner is always two-layered and thin-walled except at its tip where it may be more-layered (Text-Figs. 4–6, 34–36). The outer integument may vary in thickness. The nucellus which is massive develops a hypostase when the ovule is ripe (Text-Figs. 2 *h*, 3 *h*). Between the hypostase and the lower boundary of the nucellus occur several layers of thin-walled cells.

The vascular supply normally terminates at the chalazal region, but in exceptional cases it extends to the base of the hypostase as in *Psidium cujavillus* (Text-Fig. 42).

Megasporogenesis and female gametophyte.—The archesporial cell differentiates in the third or fourth layer of the nucellus and directly functions as the megaspore mother cell (Text-Fig. 7). It enlarges and becomes deep-seated by continued divisions of the wall cells. The first division results in the formation of two dyad cells of unequal size, of which the micropylar one may degenerate before the second division is completed (Text-Fig. 8) or both the dyad cells may undergo the normal second meiotic division (Text-Fig. 9). Thus a linear row of three or sometimes four cells may result (Text-Fig. 10). The chalazal cell alone is functional (Text-Fig. 11). It enlarges, becomes densely protoplasmic and begins to divide. The embryo-sac passes through the usual two-, four-, and eight-nucleate stages (Text-Figs. 12–14). The free nuclei organize themselves into a normal female gametophyte. The mature embryo-sac shows two pear-shaped synergids, an egg cell, two polar nuclei and three antipodal cells (Text-Figs. 15, 38). The synergids may or may not possess well-defined hooks. Abundant starch grains are present in the embryo-sac at the time of fertilization or soon after (Text-Figs. 17, 19). By the time the zygote divides, they are however depleted.

Abnormal embryo-sacs were also observed. In one instance in *Psidium guajava*, the antipodal cells closely resembled an egg apparatus while the latter simulated the antipodals; the polar nuclei lay wide apart Text-Fig. 16). Another embryo-sac showed what appeared to be two



TEXT-FIGS. 1–6. *Psidium guajava* (*ant*, antipodal; *h*, hypostase; *ii*, inner. integument; *oi*, outer integument; *nu*, nucellus; *pol*, polar nuclei). Fig. 1. L.s. young ovule showing initiation of integument. Fig. 2. Portion of chalazal part of ovule showing hypostase (*h*), degenerating antipodals (*ant*) and the polar nuclei (*pol*). Figs. 3, 4. L.s. ovules showing anomalous formation of micropyle; note the prominent hypostase below embryo-sac in Fig. 3. Figs. 5, 6. Zig-zag micropyle as seen in longisections. Figs. 1, 4–6, × 52. Fig. 2, × 72. Fig. 3, × 31.

pairs of polar nuclei besides the normal antipodal cells and an egg apparatus (Text-Fig. 17). In another instance three polar nuclei and two unorganized small nuclei were present at the micropylar end. The antipodal cells in such embryo-sacs were ephemeral (Text-Fig. 39).

Fertilization.—Fertilization is porogamous. The pollen tube is often seen to discharge X-bodies inside the embryo-sac (Text-Fig. 19). Syngamy and triple fusion occur simultaneously (Text-Fig. 18). The two polar nuclei do not fuse to form the secondary nucleus prior to fertilization. Following discharge of the sperms into the embryo-sac, fertilization of one of the polars occurs (Text-Fig. 18) before triple fusion

is completed. The zygote undergoes a period of rest during which two nucleoli of unequal sizes are observed within the nucleus of the zygote indicating syngamy (Text-Figs. 18, 20).

Endosperm.—The primary endosperm nucleus divides earlier than the zygote (Text-Figs. 19, 20). The free nuclei arrange themselves round a central vacuole (Text-Fig. 43). Accumulation of endosperm nuclei imbedded in a dense mass of cytoplasm at the chalazal end also occurs. The nuclei increase in number and may undergo repeated fusion among themselves to form large nuclei containing several nucleoli. Cell-wall formation starts from the micropylar end gradually proceeding downwards.

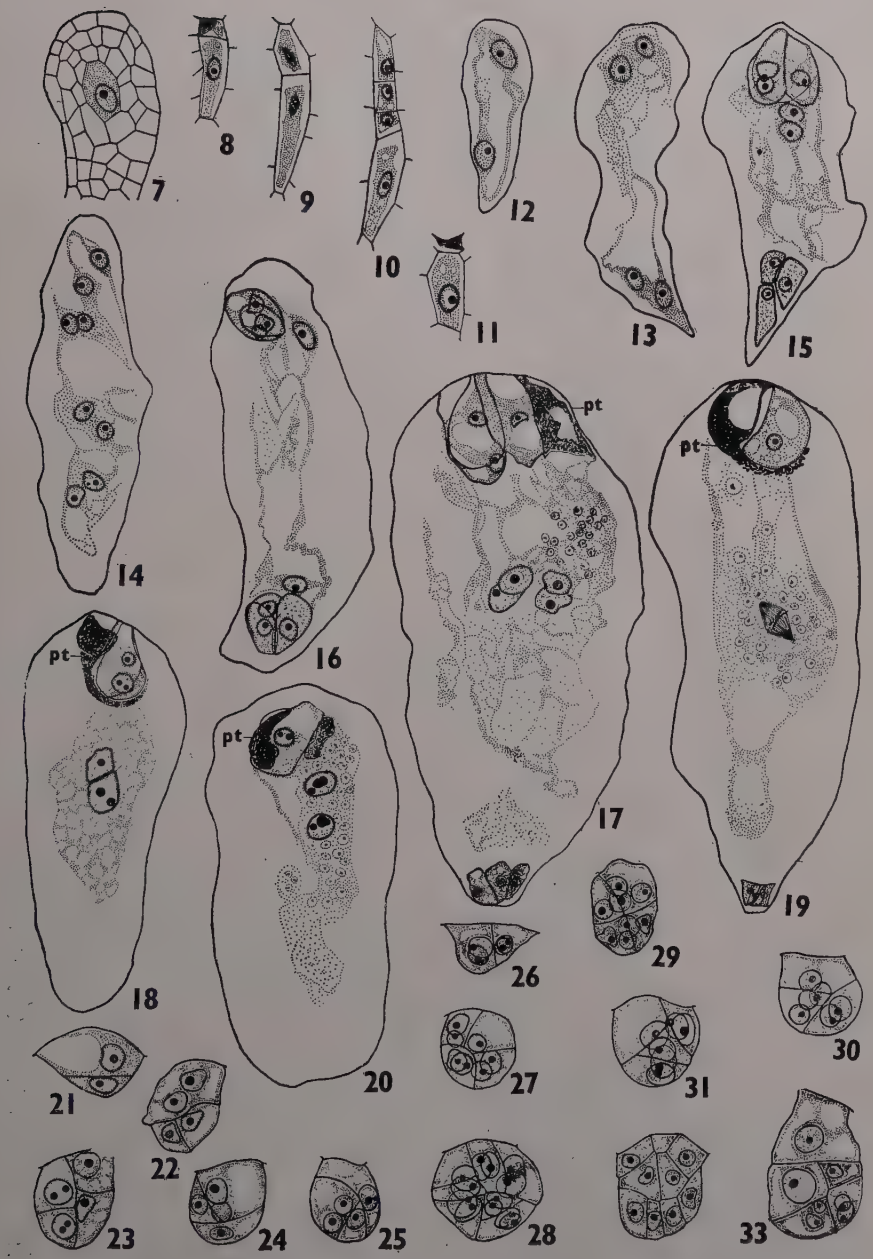
Embryo.—In *Psidium* the sequence of division of the cells in the initial stages of embryogeny is extremely irregular. The first division of the zygote is more often transverse (Text-Fig. 21) than longitudinal (Text-Fig. 26). The resultant cells again divide at right angles to the first plane of division or parallel to it. Cell divisions beyond the octant stage were difficult to follow. Text-Figures 22 to 25 show variations of cell divisions during development of the proembryo. Rarely the arrangement of the cells may be more or less regular (Text-Fig. 31). But due to divisions occurring in all planes, the eight-celled proembryo shows an irregular arrangement of its cells (Text-Figs. 27–30). Text-Figures 32 and 33 show young globular embryos in which no definite arrangement of cells nor a well-defined suspensor can be made out. However *P. cujavillus* shows a more regular arrangement of the cells in the embryo than *P. guajava* (Text-Fig. 41); and a minute suspensor may be organized by which the embryo remains attached to the micropylar part of the embryo-sac (Text-Figs. 40, 41).

In none of the hundreds of ovules examined was polyembryony ever noticed. Germinated seeds also never showed more than one seedling per seed. It appears therefore, that in the common species of guava, polyembryony does not occur nor in the species, *Psidium cujavillus.*

Discussion

Variations in arrangement of the ovules within the ovary point towards a close similarity between members of the Myrtaceæ and Onagraceæ (Johansen, 1929). The ovules of Myrtaceæ are anatropous but owing to their crowded condition may lie with their micropyle facing upwards. Such "orthotropous" or "hemi-anatropous" ovules are met with in *Psidium cujavillus.* A casual occurrence of orthotropous ovules finds its parallel in *Nesaea* of the Lythraceæ (Joshi and Venkateswarlu, 1936) and *Sonneratia* of the Sonneratiaceæ (Venkateswarlu, 1937).

The ovules are bitegminal and the micropyle is zig-zag, a feature also characteristic of the ovules of Lythraceæ (Joshi and Venkateswarlu, 1935*a*; 1935 *b*) and Melastomaceæ (Subramanyam, 1942). In *Psidium guajava* the inner integument occasionally fails to overtop the nucellus. The rim of the outer integument in such cases develops close to the inner one to form the narrow micropyle. Mauritzon (1939) has shown more or less



TEXT-FIGS. 7–33

TEXT-FIGS. 7–33. *Psidium guajava* (*pt*, pollen tube). Figs. 7–15. Stages in development of female gametophyte. Fig. 16. Abnormal embryo-sac; the antipodals simulate an egg apparatus. Fig. 17. Embryo-sac showing two pairs of polar nuclei and starch grains. Fig. 18. Syngamy and triple fusion. Fig. 19. Division of primary endosperm nucleus; observe X-bodies in the vicinity of the egg cell. Fig. 20. Embryo-sac showing zygote and two endosperm nuclei formed by division of primary endosperm nucleus. Fig. 21. Two-celled proembryo. Figs. 22–26. Four-celled proembryos. Figs. 27–33. Proembryos formed by irregular planes of division. All, ×145.

similar deviations in *Myrceugenia apiculata* and *Orthostemon sellowianus*, both of the Myrtaceæ. A general agreement in structure of the ovule in the plants under investigation with those of Lythraceæ, Melastomaceæ, Rhizophoraceæ, Onagraceæ and Combretaceæ has been observed. However, a marked difference between the nucelli of Myrtaceæ and Combretaceæ occurs. In Combretaceæ the nucellar epidermis at the upper part divides tangentially forming a "nucellar cap", a structure not present in Myrtaceæ. Tiwary (1926) and Pijl (1934) have, however, used the term in their investigations on *Eugenia*, obviously meaning the micropylar portion of the nucellus, an usage which is rather inappropriate.

In *Psidium*, the hypostase in later stages projects into the embryo-sac to form a "postament," as observed in *Cuphea lanceolata* (Mauritzon, 1934).

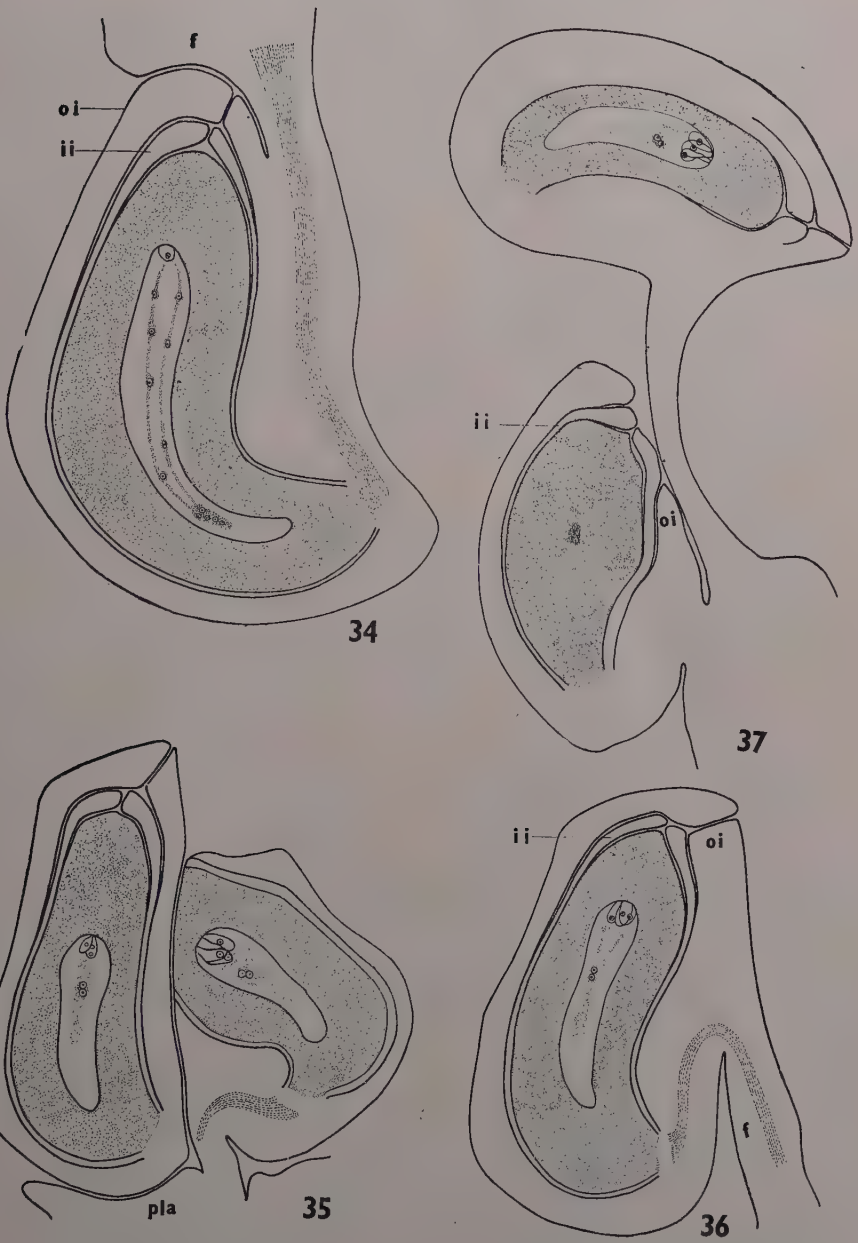
An unusual feature in the genus is the differentiation of the archesporial cell in the fourth layer below the nucellar epidermis and which functions directly as the megaspore mother cell. King (1947) working on *Punica granatum* has reported a similar development.

Meiosis in the megaspore mother cell is normal. The upper dyad cell in *Psidium guajava* may show a belated division as observed in *Cuphea* (Mauritzon, 1934). The chalazal megaspore always functions.

In structure the egg apparatus is typical and resembles those of *Rhizophora* (Cook, 1907; Mauritzon, 1939), *Peplis* (Mauritzon, 1934), *Lawsonia*, *Ammannia*, *Lagerstroemia* and *Woodfordia* (Joshi and Venkateswarlu, 1935, 1936), *Orthostemon*, *Decaspermum*, *Melaleuca*, *Callistemon*, *Tristania*, *Kunzea* and *Leptospermum* (Mauritzon, 1939), *Leandra*, *Osbeckia* and *Melastoma* (Subramanyam, 1942, 1948), *Punica* (King, 1947) and others.

Mature embryo-sacs of *Psidium* show abundant starch grains as reported also in *Lawsonia inermis* (Joshi and Venkateswarlu, 1935). Shortly after fertilization the contents diminish and by the time the zygote divides, they are absent. X-bodies similar to that reported in *Sonneratia* (Venkateswarlu, 1937) were encountered in *Psidium guajava*.

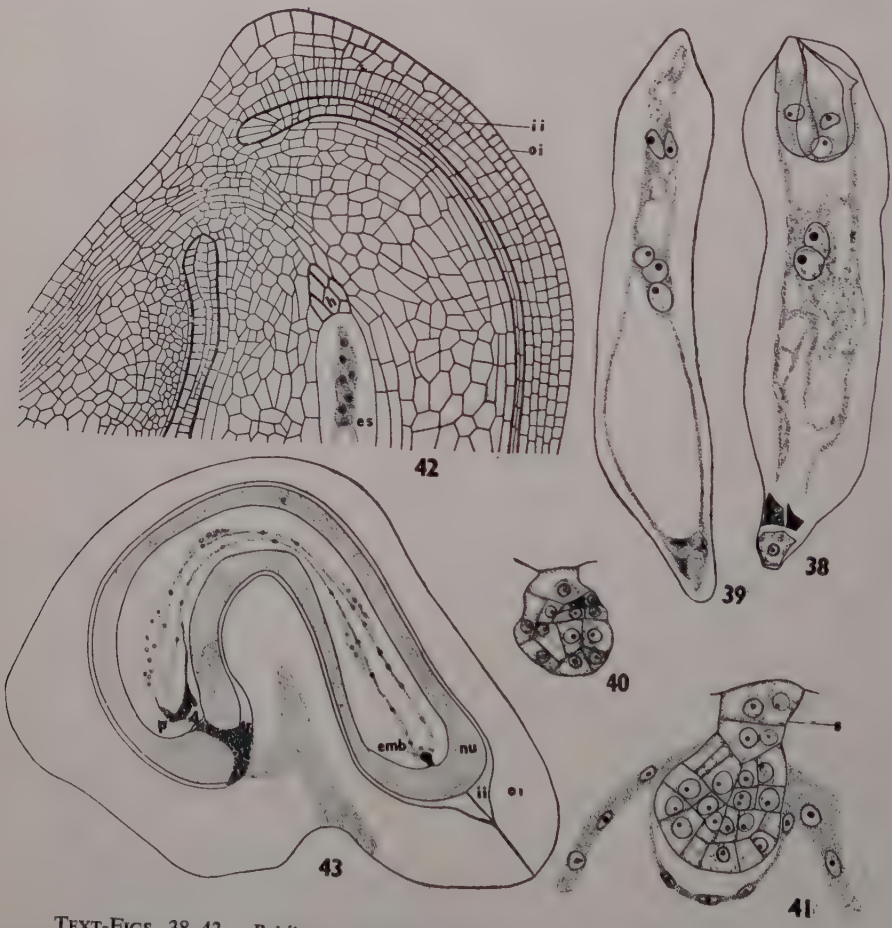
A few abnormalities in the structure of the mature embryo-sac like, reversed polarity, supernumerary polar nuclei and unorganized nuclei in the embryo-sac have been observed. Such abnormalities have been noted in the allied plants like, *Woodfordia* (Joshi and Venkateswarlu, 1935), *Zauschneria latifolia* (Johansen, 1931) and others.



TEXT-FIGS. 34–37. *Psidium cujavillus* (*f*, funicle; *ii*, inner integument; *oi*, outer integument; *pla*, placenta). Fig. 34. L.s. normal anatropous ovule. Figs. 35, 36. L.s. ovules showing 'hemi-anatropous' condition. Fig. 37. L.s. ovules, one showing a short funicle and the other, a long one; lower ovule appears sterile. **All, ×42.**

The endosperm is free nuclear to begin with, later becoming cellular. Soon after the formation of a large number of nuclei, some of them accumulate at the chalazal part of the embryo-sac, the rest forming a peripheral layer around a central vacuole in the embryo-sac as noted by Mauritzon (1939) in *Kunzea*, *Melaleuca* and *Callistemon*.

Embryogeny of *Psidium* differs markedly from that of *Myrtus* (Souèges, 1940), another member of the Myrtaceæ. While in *Psidium*



TEXT-FIGS. 38–43. *Psidium cujavillus* (*ii*, inner integument; *oi*, outer integument; *emb*, embryo; nu, nucellus; *p*, 'Postament'; *s*, suspensor; *h*, hypostase; *es*, embryo-sac). Fig. 38. Mature embryo-sac. Fig. 39. Abnormal embryo-sac showing no organization of nuclei. Fig. 40. Young globular embryo. Fig. 41. Young embryo surrounded by free nuclear endosperm; a short suspensor (*s*) may be seen. Fig. 42. Chalazal part of ovule showing elongated conducting strand near the hypostase (*h*). Fig. 43. L.s. mature ovule showing curved embryo-sac and distinct 'Postament' (*p*). Figs. 38, 39. ×138. Figs. 40, 41, ×113. Fig. 42, ×29. Fig. 43, ×7.

it is extremely irregular from the very beginning, that of *Myrtus* follows the pattern of Ranunculaceæ, *i.e.*, the two juxtaposed cells of the four-celled proembryo are derived from the terminal cell and the two superposed lower cells from the basal cell of the two-celled proembryo. The juxtaposed cells by subsequent divisions give rise to the quadrant and octant stages. The middle cell represents the hypophysis and the lowest cell divides transversely to form a short suspensor (*see* Johansen, 1950). Unlike *Eugenia* (Tiwary, 1926; Pijl, 1934) *Psidium* does not show any trace of adventive embryony.

During development of the seed coat the inner integument is completely crushed out. The outer integument becomes many-layered by the tangential division of its cells. A few inner layers of the outer integument are flattened out and the cells of the remaining layers undergo lignification. These thick-walled cells constitute the hard testa. The family Lythraceæ which otherwise shows a close resemblance to the Myrtaceæ differs from the latter in the structure of the seed coat wherein both the integuments take part.

Summary

The investigation deals with the embryology of two common species of guava, *viz.*, *Psidium guajava* and *P. cujavillus.*

Ovules are variously disposed in the ovary; it is generally anatropous save in a few cases of *Psidium cujavillus* where they are more or less "orthotropous" or "hemi-anatropous".

The ovules are bitegminal and crassinucellar; the micropyle may assume a zig-zag outline and is formed by both the integuments except in a few.

The vascular supply normally terminates at the chalazal end of the ovule; but in *Psidium cujavillus* it may sometimes traverse the nucellus and extend to the base of the hypostase.

The ovule when ripe develops a hypostase below the mature embryo-sac. The embryo-sac continues its downward growth around the hypostase which appears to project into the former forming the "Postament".

The archesporium differentiates in the fourth layer of the nucellus from top and functions directly as the megaspore mother cell. It becomes deep-seated owing to the formation of a large number of cover cells. Meiosis is normal and a linear row of triad or tetrad megaspores is formed of which the chalazal one functions.

The development of the embryo-sac is of the *Polygonum* type.

Abnormalities in the structure of the mature embryo-sac, namely, reversed polarity, supernumerary polar nuclei, unorganized embryo-sacs, etc., have been observed.

Fertilization is porogamous. Syngamy occurs normally. During triple fusion the male cell fuses with one of the polar nuclei before fusion with the second polar nucleus.

Starch grains are abundant in the ripe embryo-sac but soon after fertilization, are depleted.

The endosperm is free nuclear to begin with but becomes cellular later. A chalazal accumulation of endosperm nuclei is commonly observed in early stages. The free nuclei usually show random fusion amongst themselves and thus form giant nuclei containing several nucleoli.

Embryogeny is very irregular from the beginning and the sequence of cell divisions cannot be followed with accuracy. A suspensor is absent in *Psidium guajava* while in *P. cujavillus* a minute one may be organized. Polyembryony is completely absent in the genus.

The testa is very hard and formed by the lignification of the cells of the outer integument.

Acknowledgement

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SOME PTERIDOPHYTIC SPORES FROM THE WARKALLI LIGNITE IN SOUTH INDIA WITH SPECIAL REFERENCE TO THOSE OF SCHIZÆACEÆ

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Introduction

Tertiary spores and pollen grains from the Warkalli lignites have been recently studied by Rao and Vimal (1952) and Vimal (1953) who have described a large number of angiosperm pollen and a few pteridophytic spores. While studying the occurrence of Microthyriaceous fungi in the lignites from South India the author has come across diverse types of pteridophytic spores in the Warkalli lignite, which have not been recorded previously. The majority of these spores are beautifully preserved and possess characters which seem to be quite sharply defined and helpful in determining their affinities. Of these, the spores referable to Schizæaceæ are quite commonly represented and of many interesting types. The geological age of the Warkalli lignites is believed to be Miocene (Krishnan, 1949).

A small piece of lignite was macerated in concentrated nitric acid for about five days. It was then repeatedly washed in distilled water and treated with a 4% solution of ammonium hydroxide for about three hours. Permanent slides were made in glycerine jelly.

The sporomorphs have been classified on the lines suggested by Erdtman (1947) and wherever possible their affinities with the recent members were also indicated.

Description

Monolites Erdtman, 1947

Monolites spm. 1 (Pl. II, Fig. 1; Text-Fig. 1).—Spores yellowish, of medium size, bilateral. Lateral view concavo-convex, bean-shaped, $48 \cdot 8 \times 32 \cdot 5 \mu$. Proximal view narrow. Exospore $2 \cdot 3 \mu$ thick, surface somewhat coarsely granular.

Spores of this type are of very common occurrence in our preparations. They resemble in form, size, and exospore nature, the spores of some Polypodiaceæ (Knox, 1938; Selling, 1946; Erdtman, 1943). Spores of *Polypodium* and *Blechnum* are worth comparing in this respect.

Monolites spm. 2 (Pl. II, Figs. 2, 3; Text-Figs. 2, 3).—Spores light yellow, of medium size, bilateral. Lateral view somewhat bean-shaped,

$39 \cdot 8 \times 27 \cdot 4 \mu$. Proximal view broadly oval. Exospore intectate, $2 \cdot 4 \mu$ thick, surface verrucose. Warts (verrucæ) fairly large, and numerous; when seen laterally more or less rounded and closely placed. Warts nearer the furrow somewhat smaller than those away from it.

Spores of this type are frequently seen in our slides. They are easily comparable with the spores of *Polypodium pellucidum* (Selling, 1946). Besides they also provide some comparisons in their form and exospore ornamentation but not in size with the spores of *Phymatodes diversifolium* described by Duigan and Cookson (1956) from the Quaternary deposits in Australia. In the spores of *Phymatodes diversifolium* the warts, however, are more prominent than in the South Indian specimens.

Monolites spm. 3 (Pl. II, Fig. 4).—Spore light-brown, small, bilateral. Lateral view prominently concavo-convex, $19 \cdot 8 \times 15 \cdot 5 \mu$. Exospore intectate $1 \cdot 8 \mu$ thick, surface covered all over with prominent tubercles which at places seem to be somewhat angular.

About ten spores of this type are present in our slides. This sporomorph recalls to some extent the spores of *Polypodium alsopunctatum* (Selling, 1946). It should, however, be mentioned that the spores of the latter are larger in size.

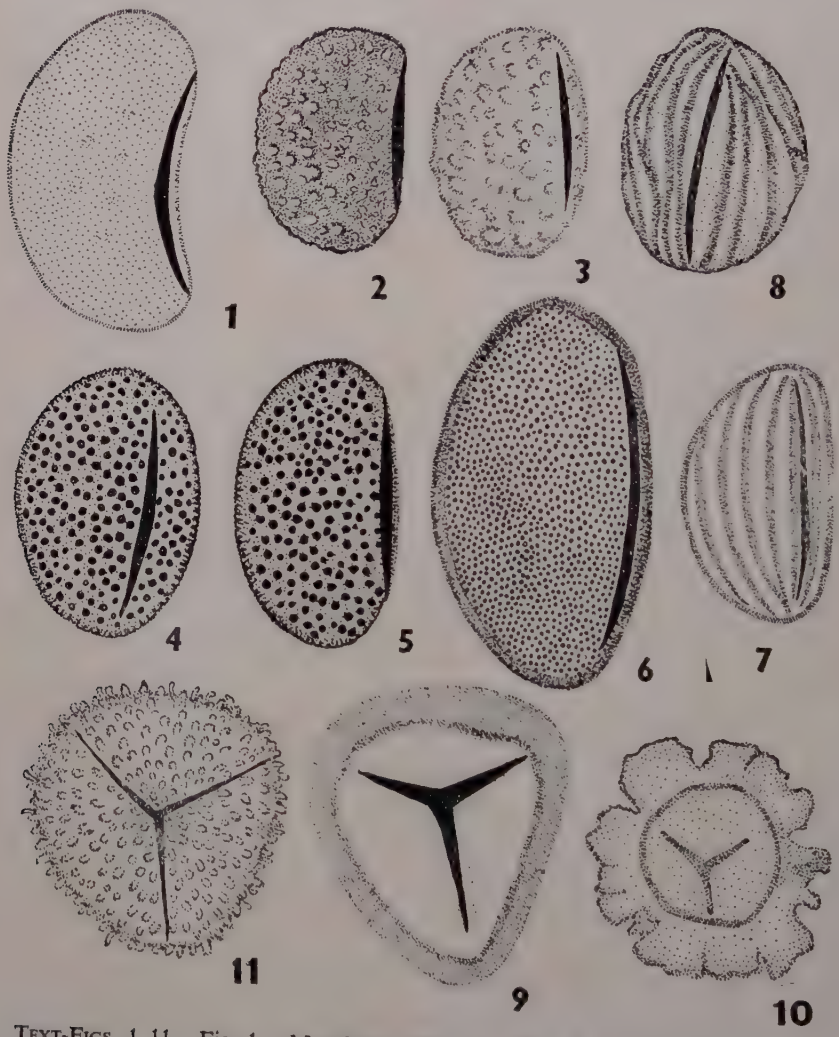
Monolites spm. 4 (*cf. Schizaea;* Pl. II, Figs. 5, 6; Text-Figs. 4, 5).—Spores golden-yellow, medium to large, bilateral. Lateral view plano-convex, $44 \cdot 2$–$50 \cdot 5 \times 24 \cdot 4$–$27 \cdot 2 \mu$ (average, $46 \cdot 5 \times 26 \cdot 1 \mu$). Furrow long reaching both the ends, broad at the middle and tapering towards the ends. Exospore $2 \cdot 5 \mu$ thick, surface heavily pitted (scrobiculate). Pits large, simple, narrow, deep and fairly spaced from each other.

Spores of this type are of very common occurrence. They show unmistakable resemblances to the spores of *Schizaea* (Wodehouse, 1935; Erdtman, 1943, Selling, 1944). In this connection it may be mentioned that the fossil spores are particularly comparable with those of *Schizaea pennula* (Selling, 1944). Some comparisons can also be made with the spores of *Schizaea punctata* (Cookson, 1956) described from the Pliocene coal of Papua. In the Papuan species, however, the spores are larger and the pits very small, more closely spaced and crowded.

Monolites spm. 5 (*cf. Schizaea;* Pl. II, Fig. 7; Text-Fig. 6).—Spores golden yellow, large, bilateral. Lateral view plano-convex, $55 \cdot 4 \times 37 \cdot 8 \mu$. Proximal view smoothly oval. Furrow thick, long, almost reaching both the poles. Exospore $3 \cdot 2 \mu$ thick, surface conspicuously scrobiculate. Pits simple, delicate, often faint, very small, numerous and crowded, narrow and deep.

These spores are also commonly met with in our slides. In their size, shape and exospore ornamentation they resemble to a great extent the spores of *Schizaea punctata* (Cookson, 1956). However, the pits in the South Indian spores are delicate and often faint while in *Schizaea punctata* they are quite prominent. In possessing delicate and often

faint pits these fossil spores show some resemblances to the spores of *Schizaea germani* (Selling, 1944).



TEXT-FIGS. 1–11. Fig. 1. *Monolites* spm. 1. Figs. 2 and 3. *Monolites* spm. 2, note the tubercles on the exospore. Figs. 4 and 5. *Monolites* spm. 4. Fig. 6. *Monolites* spm. 5. Fig. 7. *Monolites* spm. 9. Fig. 8. *Monolitos* spm. 10. Fig. 9. *Trilites* spm. 2, note the thick exospore wall. Fig. 10. *Trilites* spm 4. note the equatorial wing-like expansion of the exospore. Fig. 11. *Trilites* spm 5. All are ×800.

Monolites spm. 6 (*cf. Schizaea;* Pl. II, Fig. 8).—Spores yellowish, of medium size, bilateral, $39{\cdot}5 \times 31{\cdot}3\,\mu$. Proximal view rounded-oval. Furrow fairly wide, and long. Exospore $2{\cdot}1\,\mu$ thick, surface beauti-

fully striated. Striations (ridges) longitudinal, slightly oblique, 1·4 μ broad and seldom ramify. Dehiscence mark bordered by a single longitudinal ridge on either side.

Spores of this type are of common occurrence. In their bilateral, monoletes nature and their longitudinally striated exospore they are almost indistinguishable from the spores of many species of *Schizaea* characterized by a striated exospore (Wodehouse, 1935; Erdtman, 1943; Selling, 1944). The fossil spores show close agreement with the spores of *Schizaea palaeocenica* and *S. eocenica* (Selling, 1944) described from the Palæocene and Eocene deposits respectively of Germany.

Monolites spm. 7 (*cf. Schizaea;* Pl. II, Fig. 9).—Spores golden-yellow, of medium size, bilateral, lateral view plano-convex, 45·6×28·5 μ. Furrow narrow, fairly long, but not reaching the poles. Exospore 2·3 μ thick, surface beautifully striated. Striations obliquely longitudinal, 1·5 μ thick, occasionally bifurcate and very prominent.

Spores of this type are very common in our preparations. They show a close similarity with the spores of *Schizaea digitata* (Selling, 1944) and *S. digitatoides* (Cookson, 1956).

Monolites spm. 8 (*cf. Schizaea;* Pl. II, Fig. 10).—Spores golden-yellow, medium to large, bilateral, lateral view plano-convex, 62·3× 34·8 μ, proximal view broadly oval. Furrow fairly broad, long and rounded at both the poles. Exospore 3·7 μ thick, surface traversed by numerous obliquely longitudinal ridges (striations). Ridges closely spaced, 2·2 μ thick, frequently bifurcate and anastomose.

About a dozen spores of this type are found in our slides. While showing general similarities with various species of *Schizaea* possessing obliquely longitudinal striations, these fossil spores show no particular similarity with any of the living species.

Monolites spm. 9 (*cf. Schizaea;* Pl. II, Figs. 11, 12; Text-Fig. 7).—Spores brownish-yellow, small to medium, bilateral. Lateral view uniformly plano-convex, 28·3×20·2 μ, proximal view oval to elliptical. Furrow long, broad at the middle and narrow at the ends. Exospore 1·9 μ thick, surface longitudinally striated. Ridges straight, unbranched, 3–4·5 μ thick, few in number and widely spaced, the space between two adjacent ridges being 2·8–4·8 μ.

The spores, as a rule, possess about half a dozen longitudinal ridges. These are the smallest spores in the author's collection that may be referable to *Schizaea.* In its small size, and in possessing a few broad longitudinal ridges this sporomorph shows a cursory resemblance to the spores of *Schizaea melanesica.* However, the spores of the latter are quite different in possessing ridges which irregularly bifurcate and anastomose besides being very closely spaced.

Monolites spm. 10 (*cf. Schizaea*; Text-Fig. 8).—Spores golden-yellow, medium, bilateral. Lateral view plano-convex, 40·5×30·3 μ.

Furrow narrow, fairly long. Exospore 2·8 μ thick, surface longitudinally striated. Ridges often wavy, irregular, bifurcate and anastomose and few in number. Ridges broad being 4–5·5 μ, space between two adjacent ridges 2·1–3·8 μ.

Spores of this type are of common occurrence. As a rule, they possess 5–8 irregular longitudinal ridges. This sporomorph is similar to the above one but differs from it in being slightly larger and in its irregular, wavy often bifurcated and anastomosing ridges. When compared with the spores of the recent species this sporomorph seems to be somewhat intermediate between *Schizaea laevigata* and *S. digitata*. It also shows some similarities with the spores of *S. melanesica* (Selling, 1944). In the author's opinion the broad exospore ridges of this sporomorph no doubt indicate affinities with *S. melanesica* and *S. laevigata* which are also characterized by the same feature.

Trilites Erdtman, 1947

Trilites spm. 1 (Pl. II, Fig. 13).—Spores yellowish-brown, trilete, tetrahedral, radiosymmetric. Proximal view triangular, 30·1 × 24·6 μ. Angles rounded, sides indented or sometimes more or less flat. Triradiate mark thick, arms fairly long, more or less pointed. Exospore 1·6 μ thick, surface smooth.

This is comparable with the spores of *Gleichenia*. Spores of this type are only occasionally found in our slides.

Trilites spm. 2 (Pl. II, Fig. 14; Text-Fig. 9).—Spores yellowish-brown, trilete, tetrahedral, radiosymmetric. Proximal view subtriangular to triangular, 32·2 × 26·1 μ. Trilete mark distinct, arms long reaching the margin. Exospore considerably thick, 4–6·5 μ, surface psilate.

In possessing a thick and psilate exospore, subtriangular form and medium size this sporomorph recalls the spores of some modern Dicksoniaceæ (Selling, 1946). Some members of *Matonia*, viz., *M. pectinata* also possess somewhat similar spores (Knox, 1938), but here the spores are considerably large being about 60 μ and the exospore is finely granular. Only a few spores of this type are found in our preparations.

Trilites spm. 3 (Pl. II, Fig. 15).—Spores dark-brown, trilete, radiosymmetric, spheroidal, 42·3–46·5 μ in diam. Trilete mark sharp, arms short, narrow and pointed. Exospore 1·6 μ thick, surface finely punctate; punctations more or less symmetrically aligned around the trilete mark and of uniform size throughout.

Many specimens of this type are present in our slides. They show considerable similarity in their size, shape and exospore sculpturing with the spores of some species of *Ophioglossum*, particularly *O. nudicaule* (Knox, 1938; Selling, 1946).

Trilites spm. 4 (Pl. II, Fig. 16; Text-Fig. 10).—Spores brown, trilete, radiosymmetric, spheroidal, 25·4–35·8 μ in diam. Exospore thin, smooth and surrounded completely by a delicate equatorial wing-like expansion, thrown out into irregular folds or flaps. Triradiate mark fairly distinct, arms short, narrow and rather blunt. About 20 specimens of this sporomorph are found in our preparations.

In possessing a delicate equatorial wing-like expansion of the exospore these spores seem to be quite characteristic. They show striking similarities with the spores of *Selaginella*, viz., *S. parkeri*, *S. repestris* and *S. megastachys* (Knox, 1950). The sporomorph from the Warkalli lignite seems to be more in agreement with the spores of *Selaginella rupestris.*

Trilites spm. 5 (Pl. II, Fig. 17; Text-Fig. 11).—Spores light-yellow, trilete, tetrahedral, radiosymmetric, rounded, triangular, 30·8–34·3 μ across. Trilete mark slender, faint, arms extending to the margin. Exospore 1·8 μ thick, beset with 3–5·5 μ long, blunt rod-like processes, set 2–4 μ apart. Exospore rods often club-shaped, shorter nearer the trilete mark and longer away from it.

Spores of this type are found very commonly in our slides. The trilete mark being slender is not always distinctly preserved. These spores show a remarkable and significant similarity with the spores of *Stoifera* type of the *Selaginella* species (Knox, 1950). In their size, shape and exospore ornamentation the fossil spores are more in agreement with the spores of *Selaginella exaltata.*

Trilites spm. 6 (Pl. II, Fig. 18).—Spores yellowish-brown, tetrahedral, radiosymmetric, spheroidial, 36·5–43·5 μ across. Distal wall smoothly arched. Triradiate mark fairly distinct, arms slender, fairly long (the figure represents the distal face of the spore and hence does not show the trilete mark). Exospore 2·8 μ thick and heavily reticulate. On the apical surface surrounding the trilete mark the reticulation is delicate and broken. Meshes hexagonal, 6–10 μ, muri thick, high and projecting at the periphery up to 4·5 μ.

Spores of this type are met with only occasionally in our slides. In their trilete and tetrahedral nature, spheroidal shape and heavily reticulate sculpturing they show quite a remarkable resemblance to the spores of some species of *Lycopodium* (Knox, 1938, 1950). Knox's classical studies on the morphography of the *Lycopodium* spores clearly indicate the diversity of the ornamentation of these spores which is either reticulate, ridged, pitted or spinose (Knox, 1950). It is the reticulate type of sculpturing that characterizes the fossil spores. Based on the spore morphology the genus *Lycopodium* has been split up into four major groups, *viz.*, group *Selago*, group *Phlegmaria*, group *Verticellatum* and group *Clavatum.* Of these, it is the group *Clavatum* that is characterized by spores possessing reticulate type of exospore ornamentation. Among the group *Clavatum* the fossil spores from Warkalli show close similarities with the spores of *Lycopodium contigua* and *L. clavatum* (Knox, *l.c.*).

More or less similar spores have been recently described from the Jurassic beds of East Coast Gondwanas of India (Ramanujam, 1957). Spores of *Lycopodium sporites austroclavatidites* described by Cookson and Dettmann (1958) from the Pre-tertiary clays of Australia also show close similarities with the fossil spores from the Warkalli lignite. Because of the heavily reticulated exospore most of the specimens of this sporomorph are very finely preserved.

Discussion

Spore types referable to the modern species of *Schizaea* are commonly represented in the microflora of the Warkalli lignite. Both monolete and trilete spores are found in the family Schizæaceæ. The genus *Schizaea* is characterized by monolete spores while *Anemia*, *Lygodium* and *Mohria* possess trilete spores (Selling, 1944). It may also be mentioned that among the diverse modern species of *Schizaea* there is some variation in the exospore ornamentation, which is more or less smooth, minutely tuberculate, striated or scrobiculate. Of these the striated and scrobiculate types of spores are found in the Warkalli lignite.

Fossil *sporae dispersae* assigned to *Schizaea* have been hitherto recorded from the Tertiary of Germany, Late Quaternary deposits of Hawaiian islands (Selling, 1944, 1946), Lower Miocene to Pleistocene deposits of New Zealand (Couper, 1953), Early Tertiary deposits in South East Australia and Upper Pliocene of Papua (Cookson, 1956), and Tertiary (Miocene) lignites of Palana, Warkalli and South Arcot district in India (Vimal, 1953; Rao, 1955). The Schizæaceous spores previously reported from Warkalli are of the scrobiculate type. A single type of striated spore has been previously recorded from the Palana and South Arcot lignites.

Even a cursory examination of the diverse types of Schizæaceous spores described in the present paper would not fail to impress upon us the distinct variability in their size and exospore sculpturing and also the relation between the spore size and exospore ornamentation. In the striated spores the smallest spores are those of *Monolites* spm. 9 measuring $28 \cdot 3 \times 20 \cdot 2\,\mu$, while the largest ones are found in *Monolites* spm. 8 measuring $62 \cdot 3 \times 34 \cdot 8\,\mu$. It is interesting to note that in the largest striated spore the longitudinal ridges are numerous, narrower, often forked and closely spaced, while in the smallest striated spore the longitudinal ridges are much fewer, unbranched, broad and widely spaced. Among the scrobuculate types too one may notice that in the largest spore measuring $55 \cdot 4 \times 37\ 8\,\mu$ (*Monolites* spm. 5) the pits are small, narrow, numerous and much crowded in contradistinction to the smaller spores (*Monolites* spm. 4) with comparatively larger and less crowded pits.

According to Selling (1944) the evolutional trends of the spore characters in *Schizaea* "are clearly paralleled by a reduction of both spore sizes and exospore deposits". From this it becomes obvious

that among the Schizæaceous spores of the Warkalli lignite, *Monolites* spm. 9 represents the more advanced spore type and that *Monolites* spm. 8 as the more primitive spore type. In this connection it may be of certain interest to note that a spore similar to *Monolites* spm. 9, which on palynological grounds represents an advanced spore type, has been recently recovered from the Jurassic rocks of India (Vishnu Mittre, 1954).

The genus *Schizaea* is now a predominantly southern member, mostly distributed in the tropical zones of South America, South Africa, Australia and New Zealand. It, however, crosses the Equator in the region of South-East Asia (Selling, 1944). In India this genus is represented by two species, *Schizaea digitata* and *S. dichotoma* the former confined to the North and the latter to the South. Both Neyveli and Warkalli lignites in South India are considered to be of Miocene age. The available data indicate that *Schizaea* was more or less a common element in the Miocene flora of South India. Further, the presence of diverse types of spores referable to different modern species seems to be a significant fact, inasmuch as, it clearly points toward the occurrence of many species of this genus in South India during the Miocene age.

Although it is from the Tertiary lignites that Schizæaceous spores have been commonly recorded, it may be incidentally mentioned that spores of this family have also been reported recently from the Indian Jurassic rocks. Thus as has been mentioned already, from Nipania cherts in the Rajmahal hills of Bihar, Vishnu Mittre (1954) has described a bilateral, monoletes, striated Schizæaceous spore and from the Vemavaram shales in the East Coast Gondwanas of India Ramanujam (1957) has recorded a striated triletes Schizæaceous spore possessing small tubercular processes. These two records clearly indicate the occurrence of Schizæaceous elements in India right from the Jurassic period onwards.

Although the angiosperm types constitute the bulk of the lignite flora at Warkalli, the evidence at hand also points towards a more or less fair representation of the pteridophytic elements, consisting of such diverse families as Lycopodiaceæ, Selaginellaceæ, Ophioglossaceæ, Gleicheniaceæ, Schizæaceæ and Polypodiaceæ. Of these the members of Schizæaceæ seem to be better represented in the microflora while those of Gleicheniaceæ and Lycopodiaceæ are only occasionally met with.

SUMMARY

The present communication describes 16 types of pteridophytic spores referable to Lycopodiaceæ, Selaginellaceæ, Ophioglossaceæ, Gleicheniaceæ, Schizæaceæ and Polypodiaceæ from the Warkalli lignite in South India. Of these, spores referable to *Schizaea* are more commonly found in the microflora.

The available data indicate the occurrence of Schizæaceæ in India right from the Jurassic period onwards and that *Schizaea* was probably better represented in South India during the Miocene age than today.

Acknowledgements

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Explanation of Plate II

(All the Figures are $\times 650$)

Figs. 1–12. *Monolites* spm.

Fig. 1. *Monolites* spm. 1.
Figs. 2 and 3. *Monolites* spm. 2.
Fig. 4. *Monolites* spm. 3.
Figs. 5 and 6. *Monolites* spm. 4 (*cf. Schizaea*).
Fig. 7. *Monolites* spm. 5 (*cf. Schizaea*).
Fig. 8. *Monolites* spm. 6 (*cf. Schizaea*).
Fig. 9. *Monolites* spm. 7 (*cf. Schizaea*).
Fig. 10. *Monolites* spm. 8 (*cf. Schizaea*).
Figs. 11 and 12. *Monolites* spm. 9 (*cf. Schizaea*).

Figs. 13–18. *Trilites* spm.

Fig. 13. *Trilites* spm. 1.
Fig. 14. *Trilites* spm. 2.
Fig. 15. *Trilites* spm. 3.
Fig. 16. *Trilites* spm. 4.
Fig. 17. *Trilites* spm. 5.
Fig. 18. *Trilites* spm. 6.

STUDIES IN INDIAN SAUTERIACEÆ

II. On the Morphology of *Athalamia pinguis* Falc.*†

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Introduction

The genus *Athalamia*, one of the oldest known genera in Indian Bryology, was instituted by Falconer (1851) to include a specimen from the Himalayas (Mussoorie) which he named as *A. pinguis* Falc. The diagnostic features of the plant were drawn from scanty mature specimens and consequently lacked adequate description and illustrations. Evidently *Athalamia* failed to obtain its due recognition and in the meantime a new genus *Clevea* was instituted by Lindberg (1868) for the reception of plants which should normally have fallen under *Athalamia*. Lindberg's genus was widely recognized by bryologists and Falconer's genus eventually slumbered through about six decades after which it was again recognized by Kashyap (1915) who gave a more or less detailed account of the genus based on the same species, *Athalamia pinguis*, collected from the type locality. Subsequently, however, he (Kashyap, 1915) described also a new species *A. dioica* Kash. which he pointed out was very closely related to the former and doubtfully distinct from it.

It appears extremely surprising that the genus *Athalamia* failed to find reference in some of the classical works on Bryology by such eminent and careful workers as Leitgeb (1881) and Cavers (1910). Verdoorn (1932) and Buch, Evans and Verdoorn (1938) have recognized this genus as well as *Clevea* under "Astroporæ" although Evans (1939) later dropped *Athalamia* from Sauteriaceæ and retained only *Clevea*. Apparently through lack of due publicity it primarily persisted in works on Indian Bryology. Schiffner (1893–95) merely placed it as a doubtful genus under "Astroporæ".

In his detailed discussion of the "Cleveideæ", Bergdolt (1926, 1932) has evidently recognized this genus, has referred to the occurrence of *Athalamia pinguis* in India and has also included in his account some salient features of this plant. He, however, did not stress the affinity of the genus *Athalamia* with *Clevea*.

There has never been any doubt as to the assemblage of the genera *Clevea*, *Sauteria* and *Peltolepis* in the various schemes of classification

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in view of their wide range of similarities and their well-defined characteristics. Schiffner (1893–95) divided Marchantioideæ, after Leitgeb (1881), into Astroporæ, Operculatæ and Compositæ. The three genera were placed in Astroporæ in view of the characteristic thickenings on radial walls of cells surrounding the pore on the thallus presenting a star-shaped appearance. A similar assemblage was adopted by Cavers (1910) who also included in Astroporæ the then newly established genus *Gollaniella* (Stephani, 1905) from the Himalayas. Some years later, however, Kashyap (1929) pointed out that *Gollaniella* was generically not distinct from *Athalamia* and thus not valid. From India Kashyap (1916) instituted a new genus *Sauchia* from the Western Himalayas which showed characteristics of the Operculatæ and also reproduced in English the Latin description of *Sauteria alpina* (known from Kashmir) given by Stephani (1900). Verdoorn (1932), Buch, Evans and Verdoorn (1938) and Evans (1939) have recognized the genus *Sauchia* in their schemes of classifications.

Evans (1939), particularly, gave an excellent arrangement of genera of Marchantiales placing them in six different families. The names of the families have been derived from well-established genera falling under them. In this scheme, which is perhaps a synthesis of earlier schemes of Verdoorn (1932), Buch (1936) and Buch, Evans and Verdoorn (1938) along with inclusion of original concepts, he places the genera *Sauteria*, *Clevea*, *Peltolepis* and *Sauchia* under Sauteriaceæ.

In a recent contribution on the "Marchantiales of Japan", Shimizu and Hattori (1954) pointed out that the genera *Athalamia* and *Clevea* are congeneric and that the former predates the latter and should, therefore, be adopted. Accordingly the synonymy of all the species described under *Clevea* have been included in their publication. They have also reduced the genus *Sauchia* Kash. to a synonym of *Sauteria* Nees. These changes in the generic concepts of the two genera of Sauteriaceæ known from India have been discussed in an earlier communication by the author (Udar, 1958 *a*).

The view put forth by Shimizu and Hattori (1954) regarding the status of *Clevea* has found support in a recent classification given by Schuster (1958) in his "Annotated key to the orders, families, and genera of Hepaticæ of America North of Mexico". Schuster (1958) has adopted Cleveaceæ as the family name. It appears more appropriate to follow Sauteriaceæ as proposed by Evans (1939) since Cleveaceæ as a family name now typifies a genus no longer recognized.

Study on the members of Sauteriaceæ found in India was undertaken by the author at the kind suggestion of Prof. S. K. Pandé, D.Sc., F.N.I., F.B.S., in view of the need of clear elucidation consequent upon changes in generic concepts involved and also to provide in the hands of Indian students a first-hand knowledge of the details of the life-history of the genera of this interesting family. In an earlier communication the sporeling pattern and regeneration in sporelings in *A. pinguis* Falc. have been discussed and the present communication gives an account of the life-history of this plant.

Distribution of the Sauteriaceæ

The Sauteriaceæ are mainly holarctic and alpine in distribution with an extended range in the Mediterranean. Several of the species are apparently endemic.

Athalamia hyalina (Sommarf.) Hatt. is widely known from Europe and also in N. America from several localities enumerated by Evans (1914), *viz.*, Greenland, Ellesmere Land, North Lincoln, Quebec, British Columbia, Montana, Colorado, Idaho, Utaho, Washington and California; *A. spathysii* (Lindenb.) Hatt. from Mediterranean to Canary Islands, Palestine and North Africa; *A. andica* (Spr.) Hatt. from Andes and S. America; *A. pulcherrima* (St.) Hatt. from Abyssinia and Africa; *A. robusta* (St.) Hatt. endemic to Chile; *A. chinensis* (St.) Hatt. endemic to China; *A. trabutiana* (St.) Hatt. from Algeria; *A. handelii* (Herz.) Hatt. from N.W. Yunnan; *A. nana* (Shim. *et* Hatt.) Hatt. and *A. glauco-virens* Shim. *et* Hatt. endemic to Japan while *A. pinguis* Falc. from India and recently also reported from Nepal (Pandé and Udar, 1957 *a*); *A. dioica* Kash. and *A. pusilla* (St.) Kash. from the Western Himalayas endemic to India.

The genus *Sauteria* grows commonly in Europe and has also been reported from Greenland to N. America and Siberia, India and Japan. The widespread species *S. alpina* has recently been also identified in a collection from Nepal (Pandé and Udar, 1957 *a*). A sauteriaceous liverwort with features approaching this species has been collected by Prof. Pandé from Kandy, Ceylon, in 1939.

The genus *Peltolepis* grows in the Northern hemisphere but is comparatively rare. It ranges in Europe, Spitzbergen, Greenland, Siberia, Ellesmere Land and N. America (British Columbia) and Japan. (Hattori and Shimizu, 1955). The genus is so far unknown from India.

Quite often, as has been stated by Cavers (1910), the representative species of all the three genera, *viz.*, *Athalamia* (*Clevea*) *hyalina*, *Sauteria alpina*, *Peltolepis grandis* are found growing, often intermingled, in several localities in the Bernese Oberland.

Bergdolt (1926) has discussed at length the distribution of Sauteriaceæ. According to him: "The polar regions are considered as the original home of the Cleveideæ, and later the Cordillera. Their present distribution is either in the polar zone or in the distribution area of diluvial glaciation. Their present high alpine habitat, with the exception of the reduced Mediterranean forms, corresponds to a post-glacial withdrawal from earlier arctic areas."* In a subsequent communication Bergdolt (1932) has mapped the distribution of the various members of Sauteriaceæ.

Material and Method

Attempts have been made to collect *Athalamia pinguis* on several occasions in various stages of development. Besides some excellent

* Quoted from, *Biol. Abst.* **45**: 1930. 16033,

collections made by Prof. Pandé some recent attempts were made by the author to collect this plant from various localities. Accordingly collections were made from Mussoorie in September–October 1957 and on two occasions in Naini Tal in September–October 1949 and early in September 1958.

The plants were fixed in Randolph's modification of Navashin, form-acetic alcohol and Cornoy's mixtures (1 : 3 and 1 : 6). The material was washed, dehydrated and embedded in the usual way and sections were cut 5–12 microns thick. Staining was done in Safranin, Safranin with Fast green and Haidenhain's iron-alum hæmatoxylin. The latter gave excellent results.

Habit and Habitat

Athalamia pinguis has a very restricted distribution in the country. Kashyap (1929) described this plant from Mussoorie, Simla and Kulu but it has been also repeatedly gathered by Prof. Pandé and the author from Naini Tal as well. At these places the plants have been collected from localized pockets. They favour thin layers of soil on calcareous sandstones, exposed soils between pieces of rocks (forming walls) and often grow in shallow depressions on nearly bare exposed rocks. Their marked preference for the exposed habitats has evidently resulted in a short phase of their active existence during which they complete their life-cycle because in a collection made this year as early as the first week of September towards the last lap of torrential rains, when only short-period showers become frequent, the plants had not only matured having ripe sporogonia but had started withering up. Even at this time on exposed bare rocks, in many cases, they had already dried off showing dehisced capsules and exposing numerous prominent hyaline scales of the overturned wings of thalli. The scales provide a characteristic appearance to the rolled thallus. Under such conditions the greatly protected middle portion of the thallus still remains green.

Even though *A. pinguis* is a marked xerophytic species yet the plants often favour densely shaded spots protected by copious overgrowths of some larger plants, *e.g.*, ferns and *Selaginella* and herbaceous angiosperms. At such places the thallus retains its normal growth and expanse and may continue to grow for a much longer period.

Taxonomic Description

Athalamia pinguis **Falc.**, *Trans. Linn. Soc. Lond.* **20**: 397, 1851.

Kashyap in *Liverworts of the Western Himalayas and the Panjab Plain* **1**: 1929, Lahore.

Syn.: *Clevea gollani* Lev. in Stephani *Sp. Hep.* **6**: 5, 1917.

Monœcious, *thalli* light green, once or twice branched, 5–10 mm. long and 3–6 mm. broad, thick and fleshy, wings expanded, more or less vertical, apex narrow and rotund, tuberous; *scales* hyaline, in several rows irregularly distributed, ovate with broad expanded base

narrowing anteriorly, large, conspicuously projecting beyond margins, copious at apex and bending to protect the growing point, cells parenchymatous and uniform; *pore* elevated, surrounded by 3–8 cells with their radial walls prominently thickened; *epidermal cells* thin-walled, hyaline; antheridia dorsal, normally behind the female receptacle in 2–4 rows, often on lateral sides, often also in front and rarely on separate thallus, embedded in thallus, not organized into receptacle, scattered, male bracts absent; *female receptacle* dorsal, light to yellowish green, stalked, *stalk* hyaline, rhizoidal furrow absent, up to 1 cm. long, often larger, occasionally considerably reduced, naked, bracts subtending the receptacle similar to ventral scales though smaller and with papillæ, appressed to the receptacle, hyaline; 2–8-lobed, involucre 2-lipped, directed upward each with a single archegonium; *sporogonia* as many as lobes on the receptacle, often fewer, dark brown at maturity, splitting irregularly at the apex, valves reflexed, wall single-layered with annular thickenings; *spore* dark brown to black and opaque at maturity, 46–60 μ across the outer face, densely warty, warts prominent, 6–10 in diameter; *elaters* brown, 80–160–300 μ long, up to 10 μ broad, spirals 2–4.

The above observations are, on the whole, in agreement with those given by Kashyap (1929) but for the sake of presenting details of the plant the same has been included here.

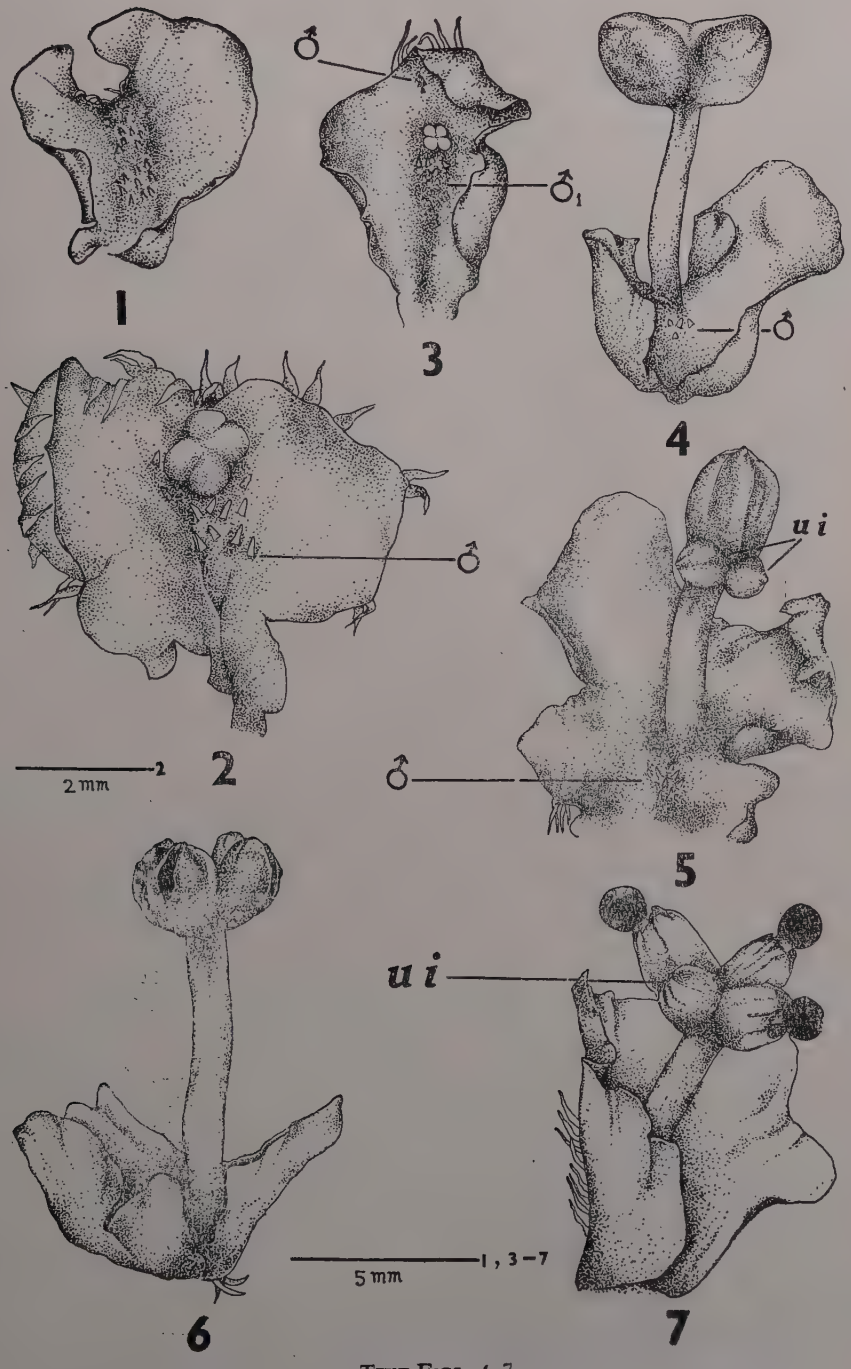
Morphological Description

Gametophyte.—A. pinguis is gregarious and normally numerous thalli grow in very close proximity together presenting a distinctive appearance. The branching is rare but is dichotomous when present. The thallus is characteristic grey green to yellow green and dorsiventral but unlike most of the other Marchantiales the dorsal surface is far from being more or less flat. The wings are thin and get upturned from a thickened midrib which is conspicuously concave dorsally (Text-Figs. 1–9).

In a section the middle part of the thallus is characterized by narrow and slit-like air-spaces (Text-Fig. 19) which become considerably oblique towards wings (Text-Fig. 20). Each chamber is bounded by unistratose filaments.

The entire thallus organization is extremely simple approaching *Riccia*. The air-spaces, however, communicate externally on the dorsal surface by pores (Text-Figs. 17, 18) which are surrounded by 3–8 cells whose radial walls are conspicuously thickened. Such thickenings on walls of these cells do not occur in all the species of *Athalamia* and, therefore, this feature is not an important generic or group characteristic as was usually regarded in the past.

Below the assimilatory zone the cells are all parenchymatous and the tissue is compact (Text-Fig. 21). A conspicuous mycorrhizal zone containing the fungus is clearly demarcated towards the base from the rest of the tissues. The mycelium is both intra- and inter-cellular and



TEXT-FIGS. 1–7

TEXT-FIGS. 1–7. Fig. 1. A male thallus. Fig. 2. A thallus with a young female receptacle and antheridia (♂). Fig. 3. A thallus with a young female receptacle and two groups of antheridia (♂, younger; ♂$_1$ older). Figs. 4–7. Thalli with mature female receptacles (*ui*, undeveloped involucres).

forms copious tangled masses (Text-Fig. 21, *mrh*). They are present in the rhizoids (Text-Figs. 22–24, *mrh*), often running in several rows, and presumably enter from the soil passing through them to the ventral cells of the thallus (Text-Fig. 21, *mrh*). The fungus is non-septate and branched. The mycorrhizal zone takes a deeper Safranin stain than rest of the tissues. Chaudhuri (1935) has given the details of the mycorrhiza in *A. pinguis*.

The rhizoids are both simple and tuberculate (Text-Figs. 22–24).

The most characteristic feature of the plant is the presence of numerous colourless large scales in several rows as in *Corsinia*. A large number of scales crowd at the apex where they bend over and protect the growing point (Text-Figs. 1–3, 8). The outer rows extend conspicuously beyond the thallus margins and are also comparatively larger (Text-Fig. 14) than those at the apex (Text-Figs. 15, 16). They are unistratose with entire margin and lack oil cells or marginal mucilage papillæ and are unappendaged in contrast to those in other Marchantiales such as *Marchantia* and *Reboulia*. "In this respect", according to Cavers (1910), "the Astroporæ recall the Corsiniaceæ and Ricciaceæ". Mucilage papillæ are, however, found in the scales subtending the female receptacle (Text-Figs. 11–13) which are considerably smaller in size than the ventral scales.

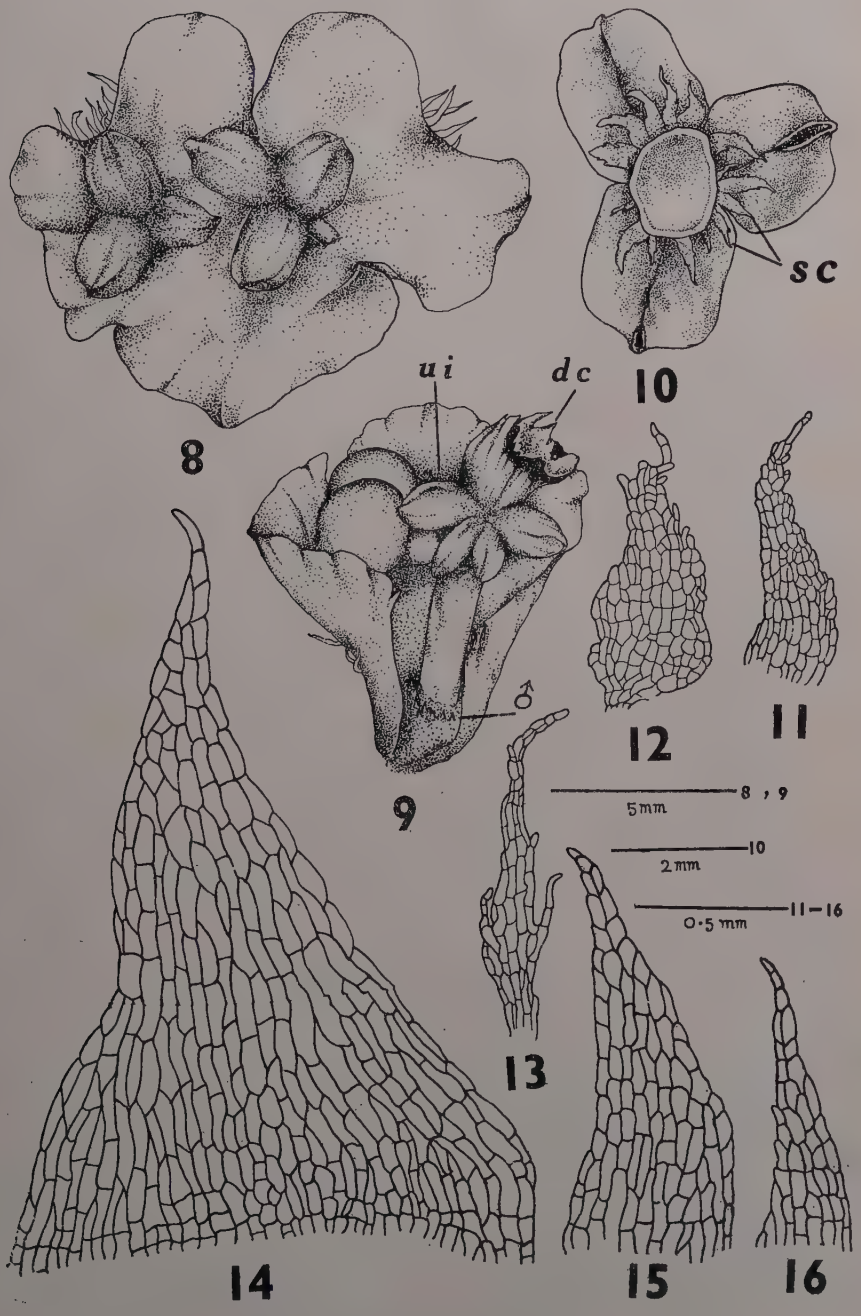
Apical Cell.—The growing point of the thallus is in the apical notch and the apical cell is wedge-shaped which cuts off four series of segments in conformity with the condition noted in most of the Marchantiales. The apical cell is triangular in shape in a vertical longitudinal section (Text-Fig. 26, *apc*) and of the two cutting faces the segments cut off on the dorsal side contribute to the formation of reproductive structures, assimilatory filaments and air pores while the segments on the ventral surface contribute to the formation of scales, rhizoids and the basal compact tissue. The segments cut off on the lateral sides of the apical cell add to the expanse of the thallus.

In transverse section of the apical region a row of four cells was noticed with dense cytoplasmic contents (Text-Fig. 25, *apc*). These are undoubtedly a group of initials and it seems reasonably certain that several apical cells function in the growth of the thallus much in the same way as has been described for *Asterella blumeana* by Peissel (1925).

The air-spaces arise schizogenously and a few cells behind the apical cell the first indication of the air-chamber is clearly seen (Text-Fig. 26, *ac*).

SEX ORGANS

Athalamta pinguis is monœcious but strictly protandrous. Quite often, therefore, a plant merely bears antheridia (Text-Fig. 1) but normally



TEXT-FIGS. 8–16

TEXT-FIGS. 8–16. Fig. 8. A dichotomously branched thallus with 2 female receptacles. Fig. 9. A thallus with two female receptacles. On the right the receptacle shows 5 involucres four of which are underdeveloped (*ui*) and one shows a mature dehisced capsule (*dc*). Fig. 10. Ventral view of a female receptacle with the scales (*sc*). Figs. 11–13. Scales from female receptacle. Figs. 14–16. Ventral scales from the thallus.

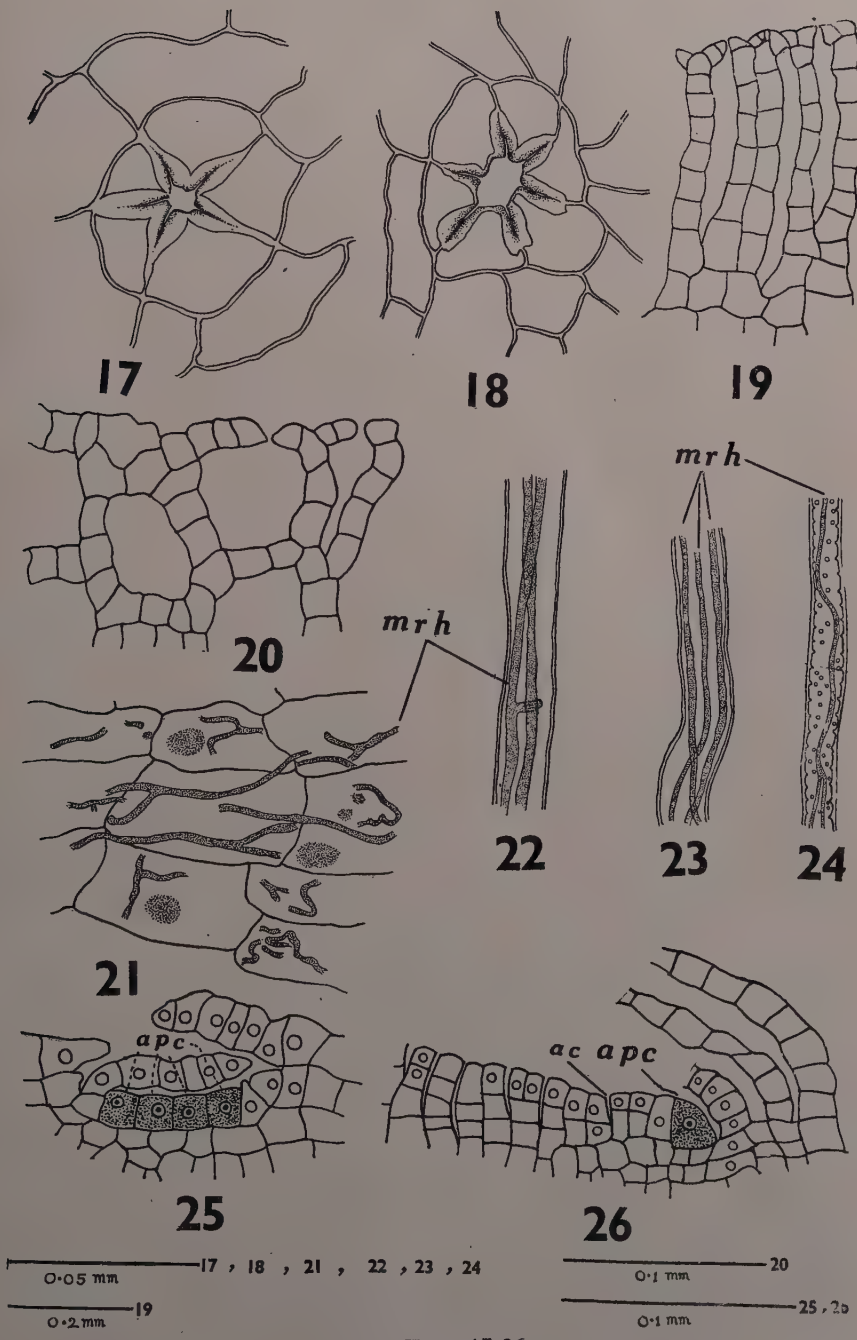
any plant, having the female receptacle, would unmistakably show the presence of antheridia usually behind it (Text-Figs. 2–6, 9).

The antheridia occur in 2–3 rows scattered along the mid-dorsal surface of the thallus (Text-Figs. 2–6, 9) and are often distributed all along the length of the thallus (Text-Fig. 1) with intervening vegetative tissue recalling in this respect the condition in *R. discolor* L. *et* L. (Pandé and Udar, 1957; Text-Figs. 3–5) or they may lie scattered behind the young developing female receptacle and usually also on its lateral sides (Text-Figs. 2, 3). Sometimes, however, antheridia may be present even towards the anterior side of the female receptacle. Subsequent to the formation of the antheridia the growth of the thallus continues and later, a little behind the apex, arises a dorsal outgrowth which gradually matures into the female receptacle (Text-Figs. 2–3). Quite often 2–3 female receptacles may occur on the thallus alternating with antheridia behind. Possibly, therefore, there is an intermittent formation of antheridia preceding the development of successive female receptacles.

The scattered antheridia also occur in *Sauteria* and most of the other species of *Athalamia*. In *Athalamia* (*Clevea*) *rousseliana*, according to Cavers (1910), there is the initiation of relatively compact antheridial grouping which culminates in organized antheridial receptacles in *Peltolepis*.

Development of antheridium.—The antheridia develop from segments of the apical cell few cells removed from it. From the stages available (Text-Figs. 27–32) it appears certain that the developmental sequence follows the usual course as in rest of the Marchantiales that have been worked out.

The antheridial initial becomes papillate and is distinguished from the neighbouring cells by its dense cytoplasmic contents. It divides transversely into an outer and an inner cell (Text-Fig. 27) the former developing into the body of the antheridium (*b*) and the latter into its stalk (*st*) much as in *Aitchisoniella himalayensis* Kash. (Ahmad, 1938). The outer cell forms a filament of three or four cells by transverse divisions (Text-Figs. 28, 29). Vertical walls then arise primarily in the basal cells and extending later in the upper ones (Text-Figs. 29, 30). The stalk cell first divides transversely (Text-Fig. 29) and then vertically (Text-Figs. 30–32) becoming two cells broad as seen in longitudinal sections. Subsequently periclinal divisions occur (Text-Fig. 31) separating an outer layer of cells which finally form the wall of the antheridium and the inner cells which by repeated divisions form a mass of spermatogenous cells (Text-Fig. 32). From the material utilized for the present investigation it has not been possible to study the details



TEXT-FIGS. 17–26

TEXT-FIGS. 17–26. Figs. 17 and 18. Pores on the thallus in dorsal view. Fig. 19. Vertical longitudinal section of a thallus in the middle. Fig. 20. Same towards the margin. Fig. 21. Same showing ventral tissue with mycorrhiza (*mrh*). Figs. 22 and 23. Simple rhizoids with mycorrhiza (*mrh*). Fig. 24. A tuberculate rhizoid with mycorrhiza (*mrh*). Fig. 25. Transverse section of thallus apex. *apc*, a group of four apical cells. Fig. 26. Vertical longitudinal section of thallus apex. *apc*, apical cell; *ac*, first air-chamber.

of the spermatogenesis. The mature antheridium is oval, pointed above and seated on a small multicellular stalk (Text-Fig. 32).

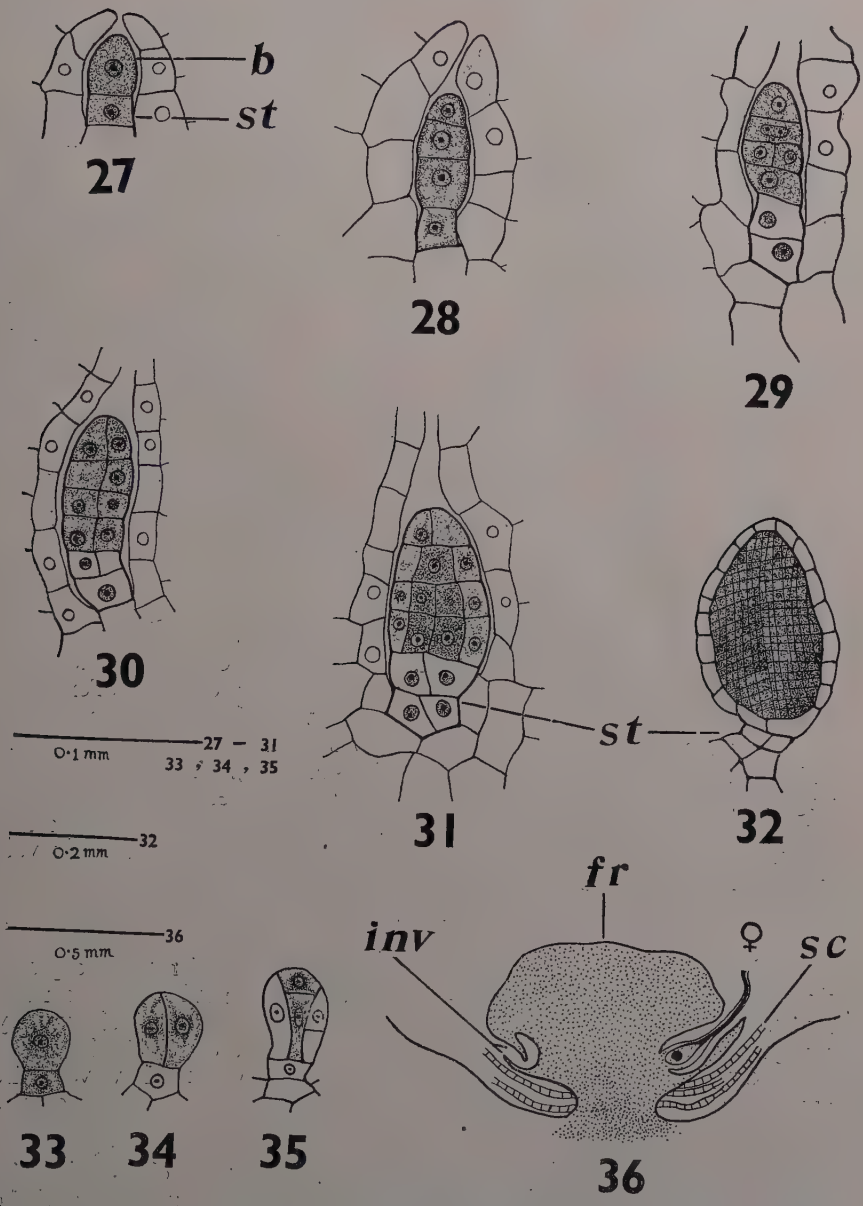
While these changes are occurring the cells in the neighbourhood of the developing antheridium divide actively and form conspicuously projected papillæ of the antheridial chamber (Text-Figs. 1–5, 9, 27–31).

There are no male bracts subtending the antheridia in *A. pinguis* as also in *Sauteria*. In *Athalamia* (*Clevea*) *hyalina*, as stated by Evans (1914), male bracts are not found although the same has been noted in this species by Bergdolt (1926).

In *Peltolepis*, however, the male receptacle is surrounded by a series of scales.

Development of Archegonia.—The formation of the archegonia is preceded by an outgrowth of the dorsal tissues in close proximity to the apex of the thallus. This results in the formation of a sessile, elevated knob-like structure (Text-Fig. 36, *fr*). Several receptacles may be formed one after another on the same thallus and since the apical cell is not utillized in its formation the growth of the thallus continues much in the same way as in *Plagiochasma*. In *Sauteria* and *Peltolepis*, on the other hand, the formation of the first female receptacle terminates further growth of the thallus. The archegonia start developing at the periphery on this cushion of tissue each getting enclosed in an involucre which is an outgrowth of the receptacular tissue. Thus in each involucre there is a single archegonium as in *Plagiochasma*. This condition is in contrast to *Sauteria* and *Peltolepis* where more than one archegonium occurs in each involucre (Cavers, 1910) although Leitgeb (1881) had earlier reported a single archegonium in each involucre in these genera. The number of involucres is extremely variable, being from 1–8 (Text-Figs. 4–7, 9) although one or more of these fail to develop mature sporogonia. The undeveloped involucres (Text-Figs. 5, 7, 9, *ui*) either show young embryos or unfertilized archegonia. The involucres project laterally presenting star-like appearance. They are pouch-like with two adherent lobes which gape out narrowly at the apex (Text-Figs. 36, 44, *inv*) and in early stages necks of archegonia project through them (Text-Fig. 36).

Active growth in the centre of the young sessile receptacle relegates the peripheral archegonia to a ventral position. The ventrally shifted archegonia have their necks curved and upturned in the proxity of the receptacular tissue with the mouth of the neck of the archegonium wide open and extending beyond the involucre (Text-Fig. 36, ♀). This is obviously an excellent adaptation for catching spermatozoids and to carry them to the eggs for fertilization. Up to the time of



TEXT-FIGS. 27–36. Figs. 27–31. Stages in the development of antheridia. Fig. 29. Shows beginning of vertical division and Fig. 31 shows periclinal division. *b*, body and *st*, stalk of antheridium. Fig. 32. Mature antheridium. *st*, stalk of antheridium. Figs. 33–35. Early stages in archegonial development. Fig. 36. Vertical longitudinal section of thallus (semi-diagrammatic) through a young female receptacle; *inv.*, involucre; *fr.*, female receptacle; ♀, archegonium; *sc.*, scale.

fertilization the receptacle is nearly sessile and pressed closely to the thallus tissues. Numerous slender and multicellular scales (Text-Figs. 10, 36, *sc*) arise below the involucres and get upturned (Text-Fig. 36). They form a protective covering round the developing archegonia.

Bergdolt (1926) has noted that the archegonial area of *Athalamia* develops from the embryonic tissue directly over the apical cells of the thallus and the archegonial area developed in this manner corresponds to a branching system whose individual branches terminate, each with a single apical cell, whose ventral segments become scales and dorsal archegonia.

According to Cavers (1910) the receptacle of *Athalamia* may be compared with "the outgrowth which arises among the archegonia in *Corsinia*" but in the former "the archegonia do not appear until the outgrowth has developed into a nearly hemispherical structure, about 0·1 mm. in diameter, and when they do appear they arise from the tissues of the outgrowth itself".

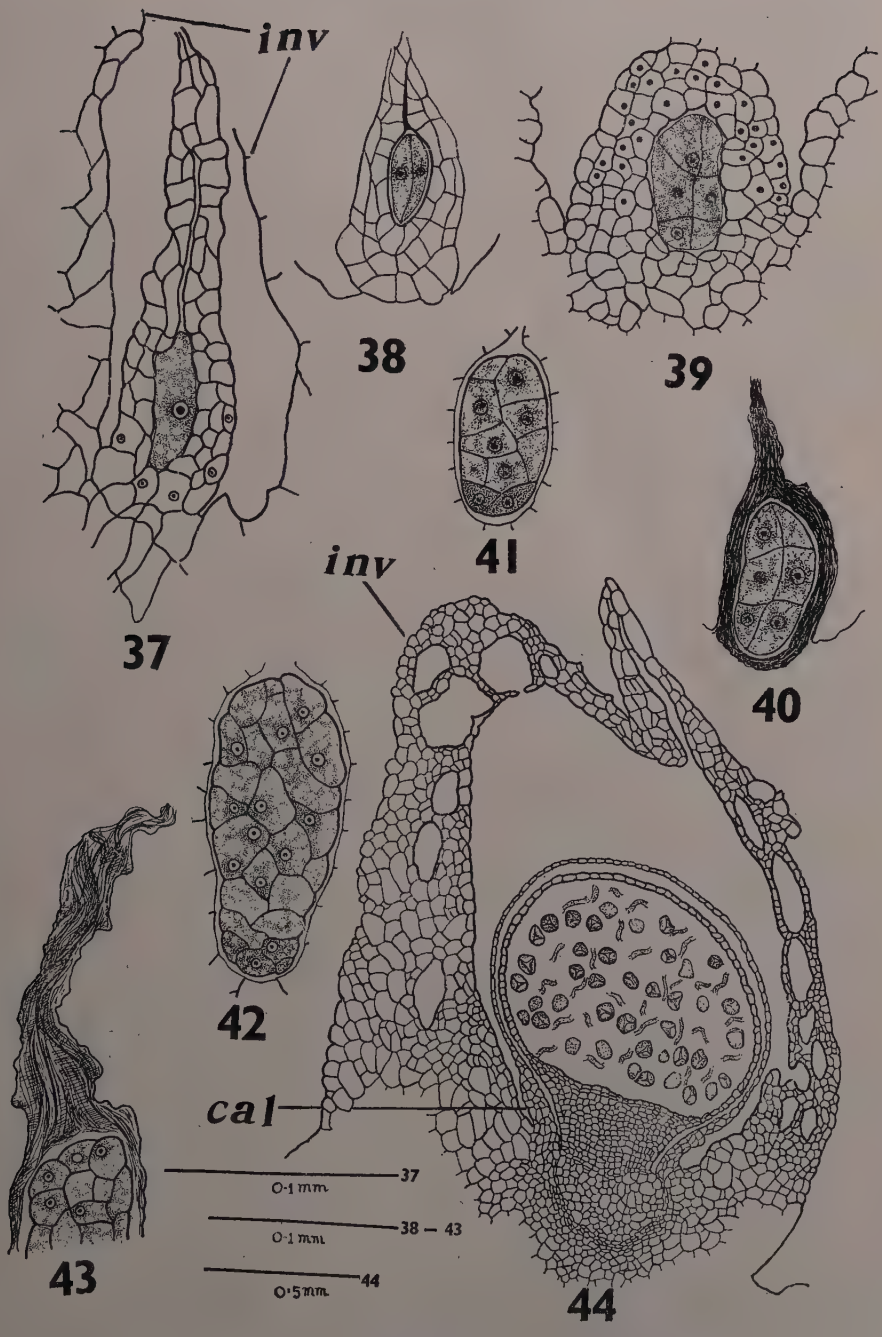
From the developmental stages of archegonia available (Text-Figs. 33–35) it is certain that the sequence corresponds closely to those already known in many other Marchantiales.

The archegonial initial becomes papillate and divides transversely into an outer and an inner cell (Text-Fig. 33). The latter apparently does not participate in the further development while the outer cell develops in the entire archegonium. There is an oblique vertical division (Text-Fig. 34) followed by another similar division (Text-Fig. 35). A third identical division also occurs with the three separating walls intersecting each other so that they surround a central axial cell and themselves lying external to it (Text-Fig. 35). The intermediate stages were not observed in the material investigated but it is certain that they are not likely to differ from the details known for other Marchantiales. A medianly cut mature archegonium was not observed in the materials sectioned.

Embryo

After the archegonia are fertilized the sessile female receptacle slowly grows into a subsessile large receptacle and a small stalk is formed. Active growth commences in the region of the latter which rapidly elongates carrying up the developing sporogonia along with the scales subtending the receptacle (Text-Figs. 4–7, 9). Often, however, the receptacle reaches maturity without the attendant elongation of the stalk (Text-Fig. 8).

While the above changes are occurring involving changes in the external organization of the female receptacle the fertilized egg and the neighbouring archegonial cells divide rapidly (Text-Figs. 37–39). The first division of the zygote is vertical to the long axis of the archegonium (Text-Fig. 38). The next stage obtained has already organized three tiers of cells (Text-Figs. 39, 40) each tier having four cells. There is a great likelihood, therefore, that after the first vertical division of the



TEXT-FIG. 37–44

TEXT-FIGS. 37–44. Fig. 37. Vertical longitudinal section through a fertilized archegonium showing the zygote. *inv.*, involucre. Figs. 38–43. Stages in embryogeny. Fig. 44. Vertical longitudinal section of a mature sporophyte. *cal.*, calyptra; *inv.*, involucre.

zygote an octant embryo is organised with two tiers as in *Asterella californica* (Campbell, 1926), *Cryptomitrium tenerum* (Haupt, 1942), *Sauchia spongiosa* (Sethi, 1931), *Stephensoniella brevipedunculata* (Mehra and Mehra, 1939), etc., following which transverse divisions in one of the tiers results in three tiers of cells. A somewhat identical condition is noted in *Anthoceros fusiformis* (Campbell, 1926) and *Notothylas levieri* (Pandé, 1934) and a more or less similar stage has been described in *Athalamia* (*Clevea*) *rousseliana* by Bergdolt (1926, Fig. 78, p. 44). There is, however, not enough justification in laying any special emphasis on the occurrence of filamentous and octant types of embryos as to their phylogenetic significance (Meyer, 1931) since there is an indescriminate intermixture of these two types in diverse genera of hepatics belonging to separate families. From his detailed investigation of several members of the Sauteriaceæ Bergdolt (1926) arrived at the conclusion that there is no set plan in embryogeny in the genera of this family.

In later stages the divisions become irregular (Text-Figs. 41, 42) but from a comparative idea drawn from the stages available it seems reasonably certain that the uppermost tier forms the capsule, the middle develops into the seta and the lowermost into the foot. Quite early in embryogeny the cells destined to form foot show denser contents and presumably are haustorial deriving nourishment from the adjoining gametophytic tissue (Text-Figs. 41, 42).

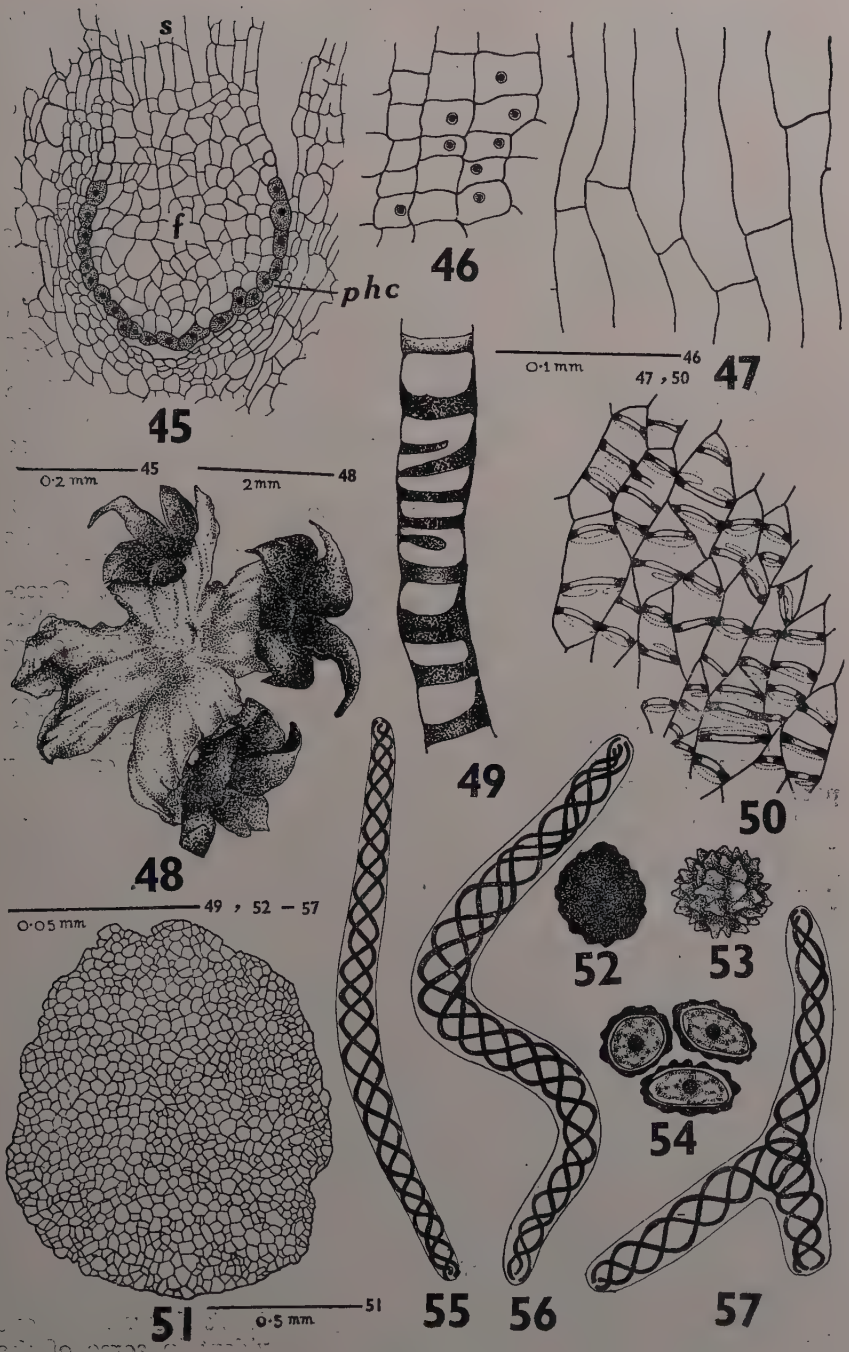
During the early stages of embryogeny cell-division is also initiated in the cells of the venter which forms a massive covering serving as a protective investment round the developing embryo (Text--Figs. 37–39). The cells of the neck also divide. The curved neck of the archegonium, in final stages, merely shrivels up and remains as an appendage (Text-Figs. 40, 43).

Text-Figure 42 shows the embryo in which there is the beginning of the periclinal divisions towards the apex which finally demarcate the outer layer of wall cells and the enclosed archesporial cells. The former remains single-layered till maturity (Text-Fig. 44) when it gets reinforced with thickened bands on radial and basal walls (Text-Figs. 49, 50).

The sporogenous cells round off and during further division there is no lobing of spore mother cells as in the Jungermanniales.

SPOROPHYTE

The mature sporophyte (Text-Fig. 44) is distinguishable into foot, seta and capsule. The foot is bulbous and its peripheral cells are large with dense cytoplasmic contents (Text-Fig. 45). They are amœboid and besides anchoring the sporophyte in the neighbouring gametophytic



TEXT-FIGS. 45–57

TEXT-FIGS. 45–57. Fig. 45. Vertical longitudinal section through foot (*f*) and seta (*s*) of a mature sporophyte. *phc*, peripheral haustorial cells. Fig. 46, Cells of seta of a young sporophyte in L.S. Fig. 47. Same of a mature sporophyte. Fig. 48. Dehiscence of capsule. Fig. 49. Wall layer of the capsule in section. Fig. 50. Same, surface view. Fig. 51. T.S. stalk of female receptacle. Fig. 52. A mature spore. Fig. 53. A young spore. Fig. 54. Spore-tetrad in section. Figs. 55–57. Elaters. Fig. 57. A branched elater. (Figs. 52–64 after Udar, 1958 *a*).

tissue help in nourishing the developing embryo by the absorption of food material. The vegetative cells adjoining the peripheral cells of the foot become crushed by the pressure of the developing sporophyte.

The seta is short and thick in early stages being narrower below and broadening above (Text-Fig. 44). The cells of the seta are parenchymatous, cubical, broader than long and with more or less dense cell contents (Text-Fig. 46). As the sporophyte reaches maturity there is a pronounced lengthening of these cells (Text-Fig. 47) so that the seta elongates and pushes the capsule out piercing through the calyptra and the involucre (Text-Fig. 7).

The mature capsule is dark black in colour. It dehisces by 4–8 irregular valves (Text-Fig. 48) which bend backwards exposing the mass of elaters and spores. The former with 2–4 spirals (Text-Figs. 55–57) are usually unbranched and attenuated at the ends. Occasionally, however, they may be branched (Text-Fig. 57). Some elaters remain attached at the apex and the base of the capsule. These are short and stumpy with lax spirals.

The mature spores are perfectly b ack and opaque (Text-Fig. 52), 65–70 μ along the maximum diameter, tetrahedral (Text-Fig. 54), reticulate with 6–8 reticulations across the outer face and prominently papillose in profile (Text-Fig. 53).

Spore germination.—Spore germination in some genera of the Sauteriaceæ have been discussed by Bergdolt (1926). According to him light is an essential factor for germination. In *Athalamia* (*Clevea*) *rousseliana* and *Sauteria alpina* a germ tube emerges which organises the germling along its axis (Bergdolt, 1926; Figs. 89, 91, 92). Recently the author (Udar, 1958 *a*) has studied the sporeling germination in *Athalamia pinguis* where, on the other hand, a multicellular germ disc is normally formed although occasionally the germ disc is organized in line with the germ tube as in *Sauteria alpina*. A very interesting feature was the formation of a germ tube from which arose the first rhizoid as in *Riccia* (Udar, 1957, 1957 *a*, 1958).

The rupture of the spore-coat in small, isolated shreds noted in *Athalamia pinguis* (Udar, 1958 *a*) occurs also in *Sauteria alpina* (Bergdolt, 1926; Fig. 91). An irregular rupture is also known in *Stephensoniella brevipedunculata* (Mehra and Kachroo, 1952).

DISCUSSION

There is hardly any doubt that *Athalamia pinguis* shows numerous features of reduction. This is conspicuously evident in some of the

trends of reduction suggested for the Marchantiales by Kashyap (1919), *viz.*, the "gradual shifting of the terminal stalk to the dorsal position by the continued growth of the thallus; the gradual elimination of the stalk; the loss of assimilatory filaments in the air-chambers; the simplification of the stomata; the simplification of the capsule wall cells and the elaters; and the decrease in the size of the seta".

The structure of the thallus in *Athalamia pinguis* is organized on an extremely simplified plan. Except for the presence of pores on the dorsal surface there is no significant difference as compared to *Riccia*. The relationship with the latter is noticed in the absence of organized air-chambers, the scattered arrangement of antheridia on the dorsal surface each embedded in an antheridial chamber and externally manifested by the prominent papillæ. The unappendaged simple scales on the ventral surface are also characteristic.

The pore in the genus *Athalamia* shows an evident series of reduction. According to Leitgeb (1881), the Sauteriaceæ (Astroporæ) are characterized by the presence of thickened radial walls of the cells surrounding the pore but this feature is by no means constant and the thickenings may even be absent in some species. Bergdolt (1926) has shown, for example, that *Athalamia* (*Clevea*) *rousseliana*, *Athalamia* (*Clevea*) *chinensis* and *Athalamia* (*Clevea*) *andina* do not show these thickenings present in some other species, *viz.*, *Athalamia* (*Clevea*) *pulcherrima*, *Athalamia* (*Clevea*) *robusta* and *Athalamia pinguis*. It is evident that no emphasis can be placed on this feature as a reliable family character.

In the dorsal position of the female receptacle *Athalamia* approaches *Plagiochasma*, a member of the Rebouliaceæ. In both the genera the thallus continues its growth after the formation of the female receptacle and several receptacles may develop one behind the other without interfering with the growth of the thallus. Evidently the apical cell of the thallus is not utilized in the formation of the female receptacle in contrast to complex Marchantiales where further growth of the thallus is arrested as the apical cell is utilized. The female receptacle has a further characteristic in having stalk devoid of any furrow and is conspicuously naked as compared to several genera of the Marchantiales which show the presence of furrow or furrows with scales and rhizoids. The receptacular tissue, although a continuation of the dorsal tissues of the thallus, is significant in the absence of pores on them and the air-spaces on the receptacular area irregularly open internally. Perhaps the greatest reduction has taken place in the presence of only one archegonium in each involucre and absence of perianth—features also shared by *Plagiochasma*. Within the members of the Sauteriaceæ the genus *Athalamia* is evidently most reduced in these features for in *Sauteria* and *Peltolepis* more than one archegonium occurs in each involucre and there is either a single furrow in the stalk (*Sauteria*) or there are two of these (*Peltolepis*).

A particularly marked tendency of reduction is seen in the mucilage papillæ in the scales subtending the archegonial areas. In this connection Bergdolt (1926) has excellently discussed a series starting from *Peltolepis* to *Athalamia*. This reduction series becomes evident since in *Peltolepis grandis* copious mucilage papillæ occur closely followed by their reduction in *Sauteria alpina*. In *Athalamia*, however, the reduction in mucilage papillæ is noticed starting from *Athalamia hyalina*, *A. rousseliana*, *A. andina* and culminating in *A. chinensis* which shows scanty papillæ.

Even the antheridial grouping shows a conspicuous tendency of reduction. In *Peltolepis* there is a definite organisation of a male receptacle (rounded cushion) while in *Sauteria*, although the aggregation of antheridia is somewhat difinite, there is no well-defined receptacle as occurs in *Peltolepis*. In *Athalamia*, however, the antheridia occur irregularly scattered as in *Riccia* but, as stated by Cavers (1910), in *A. rousseliana* there is the "first step towards the differentiation of a definite male receptacle, the group being shorter and the antheridial chambers more closely approximated to each other".

Culture investigations also afford several features of interest in this connection. In an investigation of the sporeling patterns in *A. pinguis* (Udar, 1958 *a*) it was noticed that the spore-coat ruptures in isolated shreds as has also been noted in *Stephensoniella brevipeduncula* (Mehra and Kachroo, 1952), another degenerate genus. Particularly interesting in this connection is an observation of the origin of the first rhizoid from the germ tube as in *Riccia* (Udar, 1958 *a*). The observations of Bergdolt (1926) on submerged cultures unmistakably show the trend of reduction. Under such conditions there is an inhibition in the development of thallus margins and scales associated with poor development of mucilage cells, stomata and rhizoids.

From the above discussion it is evident that the Sauteriaceæ are a highly reduced group and show graded and distinctive signs of reduction within themselves and as has also been stated by Bergdolt (1926) they represent a "phylogenetic degenerate". The genera *Peltolepis*, *Sauteria* and *Athalamia* form a natural assemblage and their inclusion under the Sauteriaceæ as adopted by Evans (1939) is best under the present state of our knowledge in contrast to the family term 'Cleveaceæ' as the latter typifies a genus now no longer recognized.

Summary

1. The morphology of *Athalamia pinguis* Falc. has been described.

2. *A. pinguis* has a very restricted distribution in the country being known from Mussoorie, Simla, Kulu and now also reported from Naini Tal in this paper.

3. The plant has upturned thin wings arising from a thick convex midrib sloping anteriorly and posteriorly in tuberous terminations.

4. The growth of the thallus takes place by means of a group of four wedge-shaped apical cells.

5. The thallus has an extremely simple organization but communicates externally by well-defined pores surrounded by 3–8 cells having thickenings on their radial walls presenting a star-shaped appearance.

6. The ventral scales are hyaline and simple. They vary enormously in size.

7. The rhizoids as well as the ventral portion of the thallus harbour mycorrhiza. The hyphæ, both inter- and intra-cellular, are aseptate and cœnocytic.

8. *A. pinguis* is monœcious and strictly protandrous. Often only antheridia develop on a thallus but the plants bearing female receptacles always show antheridia.

9. The antheridia develop more or less as in other Marchantiales. They occur scattered irregularly on the thallus and are externally manifested by prominently projecting papillæ.

10. The archegonia are produced on a receptacular tissue formed by the upgrowth of the dorsal tissues of the thallus behind the growing point. The developmental sequence of the archegonia is of the usual type of the Marchantiales. Each involucre contains only one archegonium.

11. The first division of the zygote is vertical to the long axis of the archegonium and ultimately an octant type of embryo is organised.

12. There is normally a single mature sporophyte in each involucre. Sometimes fertilized archegonium may fail to develop in one or more involucres.

13. The wall of the capsule is single-layered and is reinforced with annular thickening bands.

14. The spores are dark brown-black with prominent warts. The elaters are slender with 2–4 spirals. They may occasionally be branched.

15. The capsule dehisces irregularly into several valves each of which gets reflexed.

16. The arrangement of the genera *Peltolepis*, *Sauteria* and *Athalamia* forms a natural assemblage and best included under Sauteriaceæ as has been adopted by Evans (1939).

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OBSERVATIONS ON THE EFFECT OF THE MONSOONS IN THE PRODUCTION OF PHYTOPLANKTON*

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Introduction

It is well known that agricultural operations on land, food production especially in India, depend on the success or failure of the monsoons. Russel and Yonge (1947) while discussing seasonal cycle of plankton organisms in the tropical areas, state that "there are dry and rainy periods, the monsoons, and weather conditions that alternate with unfailing regularity during the year and it is more than probable that these secular changes may have their effect upon life in the sea". The effect of the monsoons has also been pointed out by Kow (1953) for the Malay region. In this brief account, it is proposed to show what are the effects of the monsoons on life in the sea and how they influence production therein.

Biological Year

The biological year for the Indian Peninsula may be said to commence in the middle of April or so. This is more or less the beginning of the spring in the temperate regions when life on land and water bursts into activity after the dark and dreary winter months. In India, this is about the time that the signs of the forthcoming south-west monsoon also become evident and whose outbreak and the thunder showers preceding same is eagerly awaited for the commencement of agricultural operations on land. The effect of the monsoon is felt all over the country though its intensity may vary at different places depending on the contour of the land. As applied to the sea, the biological year may be divided into (i) the south-west monsoon period from May to September and (ii) the north-east monsoon period from October to April following.

The Monsoons‡

The south-west monsoon sets in May or early in June at the southern end of the Peninsula and advances northwards striking the coast of Sind

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‡ Details regarding monsoons, currents, etc., have been drawn from Admiralty (1950) publication, and Sewell (1925, 1929).

in about 3 weeks. It is the beginning of the rainy season for most of the country. Its effect is felt more on the west coast of India and also North India, but not so much on the eastern half of South India owing to the presence of the Western Ghats. But this region also receives good amount of rainfall during the season and as most of the rivers of the country flow into the Bay of Bengal they carry lot of flood waters as there is heavy rainfall in the region of their sources also. By September, the south-west monsoon is spent but the rivers like the Ganges and Brahmaputra and the Irrawady still discharge flood waters into the Bay of Bengal.

The north-east monsoon normally begins early in the north. In the south, it becomes established only in December or so. It continues until about March. Its effect is not so much pronounced on the west coast of the Peninsula owing to the Ghats.

The west coast has a rainfall of over 100 inches; but at no locality on the east of the Ghats does the rainfall exceed 60 inches. Temperature conditions over most of the region is not very variable and there are no sharp fluctuations as far as the water is concerned.

Ocean Currents

West Coast

In the northern part of the Indian Ocean, the monsoons develop seasonal surface currents in opposite directions according to the time of the year. The east-going equatorial countercurrent, however, though lying mainly south of the Equator and extending a few degrees north of the Equator, is not reversed.

During the south-west monsoon, the coastal current in the Arabian Sea and the Bay of Bengal sets in a clockwise direction owing to the coastal conformation; and in a counterclockwise direction in November–January during the north-east monsoon. In the more open parts of the seas, the current takes the direction of a drift current due to the monsoon blowing at this time. This direction is easterly during the south-west monsoon and westerly during the north-east monsoon. The south-west monsoon circulation obtains from May–September; October is a transition month. From November onwards the current system in the Arabian Sea is as follows:—

November–January.—In the open waters the general set-up is westerly. Off the west coast of the Indian Peninsula, the predominant direction of the current to about 20° N. is north north-westerly; then, north-westerly becoming west north-westerly along the Makkram coast. Off the Arabian coast it is south-westerly.

February–April.—The predominant flow in the open waters is westerly or north-westerly. About the end of January, the counter-clockwise circulation of November–January ceases, and a coastal current in the opposite direction (clockwise) is gradually established; thus, the

coastal circulation is reversed while the north-east monsoon is still blowing. The monsoon begins to wane from the beginning of March.

The reversal of the coastal current is simultaneous along all parts of the sea. Off the Indus delta, the current is setting south. Further south, off the west coast of the Indian Peninsula, the reversal to south south-east occurs by the end of February. On the west coast the south-west monsoon is not established until June.

The reversal of the coastal current in the Arabian Sea during the latter part of the north-east monsoon is attributed to the formation of a gradient current caused by the cooling of the water at the head of the sea relatively to that farther southward. About this time (March), before the gradient current diminishes from diminishing temperature difference, the south-west monsoon begins and strengthens the clockwise coastal circulation as a normal current resulting from the wind.

May–September.—With the onset of the south-west monsoon or about its breaking, the East African Coastal Current already running in a northerly direction becomes increased in strength and constancy as also the clockwise coastal circulation in the Arabian Sea. The surface current in the open water flows in a general easterly direction everywhere northward of the west-going Equatorial Current. Often there are variations in the monsoonal drifts; however, the clockwise coastal circulation during the south-west monsoon is the most constant.

East Coast

The current circulation in the Bay of Bengal may now be considered. The year here also may be divided into periods.

June–August.—During this period, covering the commencement and a great part of the duration of the south-west monsoon, a strong surface drift flows eastward across the southern end of Ceylon between 0° and 10° S. latitude; this bends round to join the westerly flowing drift of the South Equatorial Current. The easterly drift on the north passes across the Bay of Bengal in a north-easterly direction and then east and south-east across the Andaman Sea and then through the Straits of Malacca. A smaller drift, coming from this latter channel, curves around north of Sumatra, passes for some distance south and possibly south-west along the Sumatran coast. There is a rotational movement in two of the areas; one lies close to the east coast of the Indian Peninsula extending north along the Orissa coast; the second is situated east of Ceylon. The isohaline contours suggest that there is a third movement of this nature lying off the centre of the mouth of the Bay at 4° N. and 88° E.; this is to be attributed to the current that sweeps in a north-westerly direction through the Straits of Malacca and along the north-east coast of Sumatra finally bending to the west and meeting the easterly flowing drift outside the Andaman Sea. In this, more or less, clockwise circulation in the Bay of Bengal, it is evident that the south-west monsoon coastal drift is also concerned as this carries the water around the tip of Peninsular India into the Bay of Bengal.

September–November.—This period covers the last stage of the south-west monsoon and beginning of the north-east monsoon. There are three sets of currents during this period in the Bay of Bengal: (i) Between south of Ceylon and the Equator, a strong easterly current passes which spreads fan wise at the south-east corner of the Island; part continues across the Bay of Bengal till near the Sumatran coast it becomes deflected either to the north or south; a second part bends northwards and enters the Bay of Bengal. (ii) Commencing at the head of the Bay of Bengal, a current flows towards the south-west, clearly the result of the north-east monsoon winds; it sweeps along the coast of India, reaches east coast of Ceylon and bends westwards, keeps close to the coast and reaches the Gulf of Mannar. (iii) Another current, the third, arises at the north end of the Andaman Sea and also passes towards the west and south-west; this soon after leaving the Andaman Sea is altered and by its impact with the first current, the easterly drift, a number of rotatory currents are set up in the centre and north-western parts of the Bay, in which the general trend of movement of surface mass is counterclockwise.

December–February.—The establishment of the north-east monsoon brings about great changes in the current system of the Bay. The currents show a cyclonic whirl. This is easy to recognize as it comes about owing to the influence of the north-east monsoon, the rotation of the earth and the coastal conformation. The water is driven from the Burmese coast across the Bay westwards against the Coramandal coast, becomes deflected by the coastal contour and preponderately flows north. Thus the whirl is caused. The centre of this lies 88° E. and 18° N. Constancy and current strength are now higher on the western side where the moving water mass is pressed against the coast. Between Ceylon and the mouth of the Godavari river, at approximately 17° N., the current develops and the water flows around the east coast of Ceylon into the open ocean, and some enter the Arabian Sea also.

March–May.—During this period very great changes take place in the direction of flow of the currents. During the early part of the period, a distinct double cyclonal circulation obtains at the head of the Bay, the currents moving round clockwise at two centres, 16° N. and 88° E., and 15° N. and 91° E., almost the same position as seen in December–January; at the mouth of the Bay, the currents are from east to west. With the commencement of the south-west monsoon winds in May, the cyclonal circulation disappears and the currents at the mouth of the Bay get reversed, and a well-marked surface drift from east to west is developed which bends at about the centre of the Bay and runs northwards into it. Near the Andamans the drift is in a south-west direction, a continuation of the currents produced by the north-east monsoon, while near the Nicobars, an easterly to north-easterly drift is developed.

The isohalines follow (*see* Sewell, 1928, 1929) the trend of movement of the water masses and show clearly the influence of the two monsoons on the sea-water.

Further, it may be mentioned here, that the Cold Antarctic flow, according to Carpenter (1887; *vide* Sewell, 1925, pp. 47–48) extends up to 10° N. and gradually surfaces. One arm of his flow extends to the Bay of Bengal, a second towards the Malay Archipelago and a third into the Arabian Sea. Upwelling of the waters of this current is very much augmented by the south-west monsoon winds. The influence of this bottom drift on the temperature and nutrient salt content of the Arabian Sea and other waters must be considerable. It is also known that there is an exchange of water between the Arabian Sea and Red Sea (Thompson, 1939). The foregoing review also shows that there is an exchange of water between the Bay of Bengal and Arabian Sea.

Influence of Monsoons on Phytoplankton Production

The data for nutrient salts for stations on the west coast: Bombay (Bal *et al.*, 1946), Calicut (Subrahmanyan, 1959 *b*), and east coast: Madras (Jayaraman, 1951; Ramamurthy, 1953), Gulf of Mannar and Palk Bay (Jayaraman, 1954), show that fairly high concentrations of phosphates, nitrates and silicates are present when compared with those for areas of rich production of phytoplankton elsewhere in the temperate or polar waters, particularly the values for Calicut. It is not likely that any of these nutrients acts as a limiting factor in these waters. There is no sharp seasonal fluctuation in the concentration of the nutrients on the east coast stations except silicates which register an increase during the rainy season, presumably owing to influx of freshwater. The values for all, however, keep oscillating. On the west-coast, a seasonal fluctuation is present (Subrahmanyan, 1959 *b*); but at no time, even during minima period, does the concentration go so low as to limit production.

Investigations for over 6 years on the west coast of India, at Calicut, has brought out some interesting facts (Subrahmanyan, 1959 *b*). The wind force during the months immediately preceding the south-west monsoon season, April in particular, is very high. This and the stormy conditions preceding the rainfall churn up the sea very much. The nutrient salts locked up in the mud are released in abundance into the water and these, phosphate, nitrate and silicate, and undetermined substances of organic nature, show an increase over the previous months. The organic substances are suspected to be of similar nature to those in soil decoctions and seaweed extracts which are used for promoting growth in cultures. Further, there is also an upwelling of the waters in the Arabian Sea under the influence of the south-west monsoon winds, and nutrient-laden waters are brought up and flow in the clockwise coastal circulation. The heavy rainfall helps bring down the salinity of the waters to favourable levels which together with the fall in the temperature to optimum ranges induces sexual reproduction and rapid multiplication in several Diatom species leading to the principal bloom of the year (Subrahmanyan, 1958 *a*, 1959 *a*).

After some time the quantity of phytoplankton registers a fall and the minimum is reached in November. By this time, the north-east

monsoon sets in. During this season also, phytoplankton shows one or two pulses of development, which are of a lower order when compared with the south-west monsoon bloom. The general flowering of the floral elements at this period also is brought about by the two factors conducive to that, *viz.*, a fall in salinity and temperature, the former particularly; though there is not much precipitation to affect the salinity of the water on the west coast, the lower salinity water from the Bay of Bengal entering the coastal circulation and the north-east monsoon winds bring about the favourable conditions. But the bloom is not a sustained one as salinity values go up owing to lack of freshwater influx from rivers (unlike the east coast) and reflux (*see* Huntsman, 1955) of oceanic water as a result of wind action which tends to move the surface waters away from the coast.

It has also been found, during this period, that sometimes a flowering of phytoplankton elements takes place when salinity and temperature values are also apparently not favourable. This flowering, however, does not appear to be a result of sexual reproduction and subsequent multiplication as is generally the case during the south-west monsoon season, but a result of vegetative multiplication. Such blooms are of short duration and occur during or after a period of strong winds which appear to mix up the water layers and make available certain essential growth-promoting substances from the lower layers or the bottom itself, for, there is always a good quantity of the inorganic nutrients present in the water (Subrahmanyan, 1959 *b*).

It may be particularly emphasized here that the floral elements concerned in the blooms are different each time, depending on several factors. This aspect is discussed in another paper.

Thus, on the west coast, there is a peak bloom of phytoplankton during the south-west monsoon season, occurring in July, generally; then during the north-east monsoon season, lesser pulses of development in December or January and in some years a bloom in March or April (Subrahmanyan, 1959 *a*).

Correlation of the Phytoplankton Blooms to the Monsoons—A Discussion

On the west coast of India, at Calicut (Hornell and Nayudu, 1923; George, 1953; and Subrahmanyan, 1959 *a*), at Trivandrum (Menon, 1945) and at Bombay (Gonzalves, 1947), the main bloom of phytoplankton is during the south-west monsoon season though there a slight time lag between these places depending on the time of establishment of the monsoon. A second pulse of development is not well emphasized at places other than Calicut. (Elsewhere the observations are few in number, of short durations and discontinuous, hence this remains to be determined.)

No account of plankton of the east coast so far has been of sufficient duration to enable one to assess the cycle and the factors governing the

same in a reliable manner. Nevertheless, here also, the bloom of phytoplankton may be correlated with the monsoons.

In the Gulf of Mannar, around Krusadi Island, Chacko (1950) found the period of the maximum of the Diatom population to be from June–November. In the same Gulf, near Mandapam, more detailed investigation (Prasad, 1954) showed peaks of development in March, May and October in 1950, and February, August and November in 1951. (Such small changes between the years relating to peaks of production are common on the west coast also.) Though the south-west monsoon does not bring any rain to this area, it brings about very turbulent conditions in the Gulf of Mannar (Prasad, *l.c.*) as a result of which, presumably, essential nutrients are liberated from the shallow bottom: and, though the salinity values are high due to influx of water from the Indian Ocean, a bloom of phytoplankton develops which is comparable to the bloom in March or April on the west coast, a result of vegetative multiplication of the cells. The bloom of May 1950 and August 1951 at Mandapam may have been caused in this manner. From October onwards rainfall begins in this region due to the north-east monsoon winds and salinity also records a fall. The bloom in March and October 1950, and February and November 1951 appears to be related to the effect of this monsoon of the 1949–50, 1950–51 and 1951–52 respectively. The effect of the north-east monsoon in this region is similar to that of the south-west monsoon on the west coast of India, production of phytoplankton being related to fall in salinity, temperature and increase of nutrients. Further, as seen on the west coast during the south-west monsoon in some years, on the south-east coast also, the bloom, sometimes, occurs in two pulses. The same author, during a study of the plankton in the following years, July 1951 to June 1953, found at a station in the Gulf of Mannar (G) three distinct blooms, in January, April–May and October or November; and, at a station (P) in the Palk Bay, one single prominent peak during the summer months, May–June, and another in October–November (Prasad, 1956). In these instances also, the blooms in April–May at Station G and May–June at Station P appear to be due to the south-west monsoon influence; and the peaks in January and October–November at G and October–November at P due to the north-east monsoon. The change in the timings of the blooms depend on the onset of the monsoon and also on the fall in the salinity due to precipitation and water of low salinity entering the area in the coastal circulation. It may be mentioned here that the south-west monsoon first strikes the tip of the Peninsula and advances northward, and the stations in the Gulf of Mannar and Palk Bay are farther south of Calicut (between 9° 13′–9° 20′ N. and 79° 05′–79° 15′ E.) where, obviously, the effect of the monsoon will be felt much earlier. Further, it may be noted that the period of bloom of phytoplankton in this area is nearer to the transition months between the monsoons when there is a change in the direction of the winds and currents. The Gulf of Mannar and Palk Bay are shallow seas, the depth varying from 2½–6 fathoms only; naturally, therefore, wind may have a great role in influencing the production of phytoplankton as in the Great Barrier Reef region (Marshall 1933; *see* also Subrahmanyan, 1959 *b*).

Two sets of observations are available for the Bay of Bengal off Madras, one published in 1931 (Menon) and the other 22 years later in 1953 (Ramamurthy).* According to Menon, the general maximum which occurs in April–May is a culmination of a regular and constant Diatom increase beginning in the September preceding, though there is a subsidiary peak in December. According to Ramamurthy, Diatom production is rich in February, April, May, August, September, November and December. The two accounts are comparable except that Ramamurthy records high production in August–September; in fact, in the first year of his observation, this peak is of a higher order than the April–May production. Unfortunately, neither of the accounts contain data even for two full years; how far the cycle would repeat itself cannot be judged. Nevertheless, it is seen that there are pulses of production during south-west and north-east monsoon seasons. The poorest month for plankton here appears to coincide with the period of the reversal of the coastal current, September–November (south to north flow in the earlier period becoming north to south, Sewell, 1929), resembling conditions in November on the west coast. Though the south-west monsoon does not bring any rainfall to this region, its effect is widespread throughout the rest of India so much so, owing to the heavy rainfall at the sources of the large river systems of India, an enormous quantity of water comes to be discharged into the Bay of Bengal and even after September this continues. From June–August this effect through river influx appears to be not felt at Madras since the coastal circulation at this time tends to move the water away from the region and in a northerly or north-easterly direction and brings in also water of a higher salinity from the Indian Ocean in the south. Only after September, with the reversal of the current bringing in water of a lower salinity also from the north and the setting in of the north-east monsoon, optimum salinity values appear to be reached leading to pulses of phytoplankton production. After recording a fall in the standing crop in January, the Diatom population increases again leading to another peak in April or May. It does not appear to be certain yet when the main production occurs at Madras; continuous work for several years appears to be needed here.

At Vizagapatnam, data are available only for about two years (Ganapati and Rao, 1953; Ganapati and Murthy, 1955). Here also, two pulses of production are reported, a "spring" maximum in February-April and an autumn one in October–December. The accompanying figure (Ganapati and Murthy, 1955, p. 92, Fig. 2) shows the Diatoms attaining a peak in April, the quantity falling till September to a low crop and two smaller peaks in November and February after the scarce period in September and October. The *standing crop*, as seen from the figure, is of a higher order from April–August, even after the fall from the maximum, than even the secondary peaks in November and February. While Madras and regions south of it do not have any appreciable rainfall* during the south-west monsoon, Vishakapatnam receives its major

* Data relating to Meteorological conditions, etc., were obtained by courtesy of the Director, Regional Meteorological Centre, Madras. Data not quoted here in order to save space.

portion of rainfall during this season and also some in October, November and December of the north-east monsoon period. The "spring" bloom at Vishakapatnam begins when the pre-monsoon showers occur there and a high standing crop is maintained from April–August; this would have been of a higher order and of prolonged duration if the salinity had not fallen to a very low level in the following month owing to the local precipitation as well as discharge of rivers in the environment and the change in the current circulation also bringing in water of low salinity. On this coast, as on the west coast, the standing crop is of a higher order from May –August with a number of pulses of development during the north-east monsoon period.

It is interesting to note that while there are several species of Diatoms and other phytoplankton elements common to both the Arabian Sea and Bay of Bengal, quite a good number are not so* (Subrahmanyan, 1946, 1958 *b*). This may be due to salinity conditions; salinity values, on the whole, are of a lower order in the Bay of Bengal and quite a good portion of the Bay may be considered estuarine. In the Arabian Sea, conditions are more oceanic and a higher salinity prevails, probably also due to the influx of Red Sea water into the Arabian Sea, besides the waters from the equatorial region.

It is not clear how far the discharge of the rivers into the sea around the Indian Peninsula contributes to its fertility. Differing views exist on this aspect and it would seem that no generalization is possible for all the nutrient salts; conditions may differ according to the area and nature of land over which the rivers flow and the effect of the effluents flowing into them before they reach the sea. For the west coast of India, there is some evidence for an enrichment of the sea by freshwater influx; it has also been found that the sea bottom mud definitely contributes to the enrichment of the water and concentration of some of the salts (Subrahmanyan, 1959 *b*). For instance, phosphate content of the water and the bottom mud have been shown to have an inverse ratio (Seshappa, 1953); this confirms an exchange of substances between the bottom mud and the water. The changes connected with mud-bank formation, caused perhaps by the south-west monsoon and currents, also appear to exercise considerable influence on the fertility of the waters (*see* also Panikkar, 1952, p. 756).

Sewell (1952) also refers to the high fertility of the waters of the Arabian Sea and after discussing the richness of the fauna (*l.c.*, pp. 714–15) and the high percentage of organic matter in the bottom deposits of that sea, he states (*l.c.*, p. 716): "The origin of this high percentage of organic matter in the bottom deposit is to be found in the amazingly rich zooplankton that is present, along the African and Arabian coasts and extending eastward towards India, during the months of the south-west monsoon and shortly after. The cause of this rich plankton is to be found in the upwelling of deep water all along the coasts of East Africa and

* An account on the qualitative and quantitative distribution of the various species of Diatoms and Dinophyceæ is under preparation.

Arabia under the influence of the south-west monsoon wind. The upwelling water is rich in nutrient salts, nitrates and phosphates, and thus provides the necessary conditions for a rich outburst of phytoplankton that is followed by an amazingly rich zooplankton; and as the dead bodies of these organisms sink to the bottom and accumulate in the mud, they provide nutriment for large numbers of other animals in the zones above and below the azoic region where there is sufficient oxygen to support life."

For the east coast of India, unfortunately, there have been no intense and continuous investigations of the sea-water and that of the large river systems. There is a probability that for this region, there may be a definite contribution by the rivers concerned, as they are large and flow through vast areas carrying an enormous quantity of silt and might contribute to the enrichment of the Bay of Bengal as does the river Mississippi of North America to the Gulf of Mexico (Riley, 1937–38). The blooms of phytoplankton may bear a closer relationship to this factor which in turn is linked with the monsoons. It may be mentioned here that upwelling of water has also been demonstrated off Vishakapatnam coast (La Fond, 1954).

From the above review, the correlation between the monsoons and production of phytoplankton in the Indian waters becomes evident. Obviously, the sequence is brought about by the effect of the monsoon winds mixing up the water layers and the sea bottom besides bringing about precipitation and also the movement of the water masses. It is clear from the data for current circulation in the Arabian Sea and Bay of Bengal that there is an exchange of water between them and also other regions such as the Indian Ocean, Red Sea and the Antarctic. The isohalines (Sewell, 1929) follow the trend of the movement of the water masses and show clearly the influence of the monsoon rainfall on the sea-water. These factors also bring about an increase in the nutrient salts and the cumulative effect is conducive to phytoplankton production. Thus, the fertility of the Indian coastal waters also, it would appear, is dependent on the monsoons as is agricultural production on land.

Summary

An account setting out the influence of the south-west and north-east monsoons on the hydrological conditions and thereby on the production of phytoplankton is given with reference to the writer's work on the west coast of India and several other investigations on the west and east coasts of India. The correlations of the phytoplankton blooms at the different places to the monsoonal period are pointed out and discussed. The fertility of the Indian waters appears to be controlled by the monsoons.

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EFFECT OF MALONIC ACID ON RESPIRATION

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Introduction

Work has been in progress in these laboratories on the acid metabolism of succulent and non-succulent plants for some time. Many of the typical features of "Crassulacean acid metabolism" have been observed by Seshagiri and Murty (1957) in *Ananas sativa* and by Seshagiri and Narasimham (1957) in *Billbergia* sp. Some of the acids of the Krebs TCA-cycle have also been identified in these plants. The present investigation was taken up to find evidence for the existence of Krebs cycle and to study the nature of intermediary acids of TCA-cycle with the help of inhibitors in some succulent tropical plants.

In studies on the mechanism of respiration of tissues selective inhibitors have come to be used to a large extent in recent years. Though it has not yet been possible to pick out a single specific inhibitor for each enzyme, there are a number of chemicals which under appropriate conditions and dosages react preferentially with particular enzyme systems. Malonic acid is one such substance, which is assumed to inhibit succinic dehydrogenase specifically. This acid has as such been used to demonstrate the existence of intermediate acids of Krebs cycle during the changes taking place in respiration.

Thunberg (1909) was the first to record the depressing effect of malonic acid on respiration. Later Quastel and Whetham (1925) observed a retardation in the rate of dehydrogenation of succinic acid by resting bacteria, in anaerobiosis at pH 7. Though some workers (Hopkins *et al.*, 1938) have tried to explain the nature of malonic acid inhibition of succinic dehydrogenation, it should also be noted that malonic acid should not be regarded as a specific inhibitor of succinic dehydrogenase for it has been reported to inhibit lactic dehydrogenase (Quastel and Wooldridge, 1928; Cook, 1930 and Das, 1937) and dehydrogenation of malic acid. Still there is another suitable method of demonstrating the specificity of an inhibitor and that is by the reversal of inhibition. In these investigations work along this line also has been planned to elucidate this problem of malonic acid inhibition. The literature on this subject has been critically reviewed and discussed by Hanly *et al.* (1952) who have further shown the importance of pH in malonic acid inhibition in carrot root respiration.

Materials and Methods

Investigations were carried out on eight plants belonging to three families namely Crassulaceæ, Bromeliaceæ and Begoniaceæ.

Experiments were conducted on mature leaves collected in the morning, care being taken to pick-up the fourth leaf from the tip always. Gaseous exchanges were measured on fresh weight basis and in all experiments, 0·25 g. of leaf tissue was used. Thin and uniform sections of about 0·2 to 0·3 mm. in thickness were prepared with the accurately weighed tissue and these slices were used.

Molar solutions of malonic and succinic acids were prepared to the required concentrations and the pH adjusted to 4·0 with NaOH. This pH was chosen as Hanly *et al.* (*loc. cit.*) have shown that malonate is effective as a respiratory inhibitor only at pH 4·0. Distilled water was taken as the medium for all these experiments. The pH of the medium after experiment was tested and it was always between 4·0 and 4·5 at the end of each experiment.

Gaseous exchanges were measured by the two-vessel method of Warburg (Dixon, 1951) maintaining the temperature of the thermostatic bath at 30° C. One ml. of the inhibitor was directly added to the tissue in the reaction flask before the experiment was started, to develop its inhibitory effect. Additions were made from the side arm in reversibility experiments and here 1 ml. of succinic acid also was added. Respiratory measurements were carried out for three hours after equilibration and the amounts of the gas absorbed or evolved were calculated (Dixon, *loc. cit.*).

The effect of different molar concentrations of malonic acid (0·01 M to 0·05 M) on oxygen uptake and CO_2 evolution in eight different plants was evaluated. The plants investigated were *Ananas sativa*, *Billbergia* sp. and *Pitcairnia* sp., of Bromeliaceæ, *Bryophyllum calycinum*, *Kalanchae* sp., *Bryophyllum tubuliformis* and an unidentified *Bryophyllum* sp., of Crassulaceæ and *Begonia anamalayana* of Begoniaceæ.

The data collected on gaseous exchange by different tissues under varying concentrations of malonic acid are expressed in terms of the c.mm. of gas absorbed or evolved per gm. fresh weight of the tissue per hour and also in terms of percentage of inhibition or acceleration as the case may be, using the control value as the normal value.

Experimental Findings

(1) *Effect of malonic acid on the oxygen uptake of tissues.*—From the data collected (Table I and Text-Fig. 1) it may be observed that the $Q^{FW}O_2$ (quantity of oxygen absorbed/G.F.Wt./ hour) varies considerably in the different tissues studied. In some plants malonic acid caused a clear cut and continuous depression in oxygen uptake, while in some a definite increase in oxygen absorption was observed.

In *Ananas sativa* the control value of $Q^{FW}O_2$ was 48·5 c.mm. and on treating the tissue with 0·01 M malonic acid the value rose to 80·2 c.mm., the percentage of increase over the control being 65·3. Further

increase in the concentration to 0·02 M did not effect any further acceleration. With 0·03 M malonic acid a depression in O_2 absorption was observed but the value was still 24·6 per cent. higher than the control. Further decline was noticed with increase in concentrations until a depression of 75·9 per cent. was observed at the 0·05 M level, when compared to the control value.

TABLE I

Effect of malonic acid on respiration of different tissues

Name of the plant	Molar conc. of malonic acid M	C.mm. of O_2 absorbed G.F.Wt./Hr.	Acceleration (+) or inhibition (−) over the control in %	C.mm. of CO_2 evolved/ G.F.Wt./Hr.	Acceleration (+) or inhibition (−) over the control in %
Ananas sativa	0	48·5	0	65·1	0
	0·01	80·2	+65·3	88·7	+36·2
	0·02	80·2	+65·3	116·1	+78·3
	0·03	60·5	+24·6	73·3	+12·4
	0·04	52·1	+ 7·8	55·7	−14·4
	0·05	11·7	−75·9	33·7	−48·2
Pitcairnia sp.	0	33·7	0	42·7	0
	0·01	45·1	+33·8	52·2	+22·2
	0·02	61·7	+83·1	75·0	+75·6
	0·03	45·1	+33·8	51·5	+20·6
	0·04	35·7	+ 5·9	63·7	+49·2
	0·05	21·1	−37·1	26·7	−37·5
Begonia anamalayana	0	51·6	0	83·3	0
	0·01	65·5	+26·9	78·0	− 6·4
	0·02	39·0	−22·5	60·9	−26·9
	0·03	33·6	−34·9	48·8	−41·7
	0·04	30·5	−42·9	50·9	−38·9
Billbergia sp.	0	63·6	0	77·3	0
	0·01	56·6	−11·1	65·5	−15·1
	0·02	45·9	−26·9	53·2	−31·2
	0·03	43·6	−31·4	77·4	+ 0·1
	0·04	41·5	−34·6	69·6	− 9·9
	0·05	30·4	−52·1	51·6	−33·2

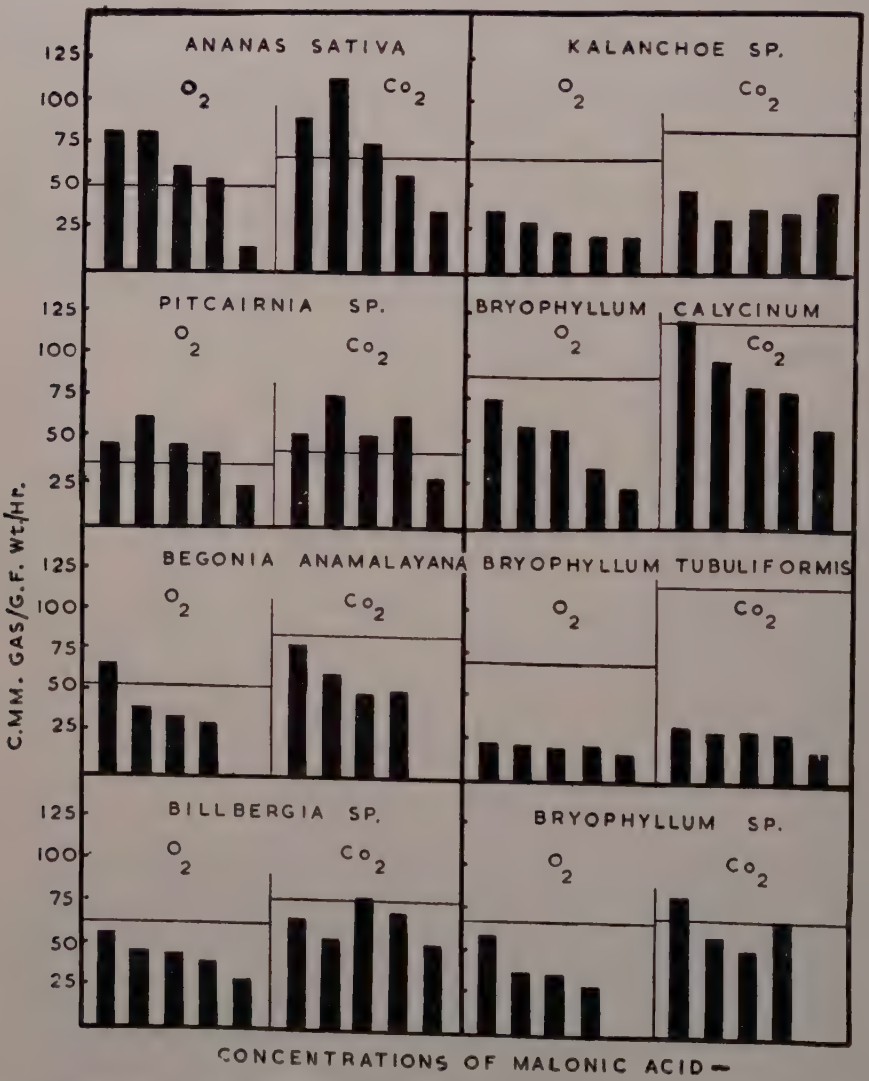
TABLE I (*Contd.*)

Name of the plant	Molar conc. of malonic acid M	C. mm. of O_2 absorbed/ G.F.Wt./Hr.	Acceleration (+) or inhibition (−) over the control in %	C. mm. of CO_2 evolved/ G.F.Wt./Hr.	Acceleration (+) or inhibition (−) over the control in %
Kalanchoe sp.	0	65·2	0	81·7	0
	0·01	35·6	−45·4	47·3	−42·1
	0·02	28·8	−55·8	31·7	−61·2
	0·03	22·3	−65·8	40·5	−50·4
	0·04	20·7	−68·3	29·2	−64·3
	0·05	19·2	−70·8	47·3	−42·2
Bryophyllum calycinum	0	88·0	0	121·2	0
	0·01	74·9	−14·9	122·3	+ 0·9
	0·02	59·3	−32·6	98·1	−19·1
	0·03	57·7	−34·4	83·9	−30·8
	0·04	35·0	−59·1	81·3	−32·9
	0·05	22·7	−74·7	59·5	−50·9
Bryophyllum tubuliformis	0	69·5	0	115·7	0
	0·01	22·5	−67·6	32·5	−71·9
	0·02	21·8	−68·7	29·1	−74·8
	0·03	20·4	−70·7	31·5	−72·8
	0·04	21·8	−68·7	29·9	−74·2
	0·05	16·8	−76·9	18·7	−83·8
Bryophyllum sp.	0	66·3	0	68·9	0
	0·01	58·4	−10·4	82·2	+19·3
	0·02	37·0	−42·4	58·5	−15·1
	0·03	36·0	−45·6	50·8	−26·3
	0·04	28·8	−55·1	68·8	− 0·2

In Pitcairnia sp. also a similar trend in response to different concentrations of malonic acid was observed. In these two cases the value for 0·03 and 0·04 M concentrations of malonic acid were still higher than the control and it was only in the highest concentration (0·05 M) used that any depression, when compared with the control, was observed. In *Begonia anamalayana* also a slight rise was observed at 0·01 M concentration and further increase in malonic acid concentration inhibited O_2 absorption to levels lower than the control.

In the rest of the plants experimented upon the effect of malonic acid was entirely different, because in these plants addition of malonic acid depressed the rate of O_2 uptake. In *Billbergia* sp. the percentage

of inhibition in 0·01 M concentration when compared with the control was 11·1 and in the highest concentration used it was 52·1 per cent. Similar inhibitory effect of malonic acid was also observed in two other plants— *Bryophyllum calycinum* and *Bryophyllum* sp., and in these plants inhibition with increasing concentration of malonic acid was slow and progressive.



TEXT-FIG. 1. The effect on the oxygen uptake and carbon dioxide output on addition of 0·01, 0·02, 0·03, 0·04, 0·05 molar concentrations of malonic acid to different respiring tissue slices. Horizontal lines are the values obtained for tissues to which no malonic acid was added (control values).

On the other hand, with *Kalanchoe* sp. and *Bryophyllum tubuliformis*, a sudden fall in oxygen absorption was observed even in the lowest concentration (0·01 M) of malonic acid used which appeared to be another variation in the inhibition effect at 0·01 M level in these investigations. The percentage inhibition in *Kalanchoe* was 45·4 and in *Bryophyllum tubuliformis* it was 67·6 at the 0·01 M level. In *Bryophyllum tubuliformis* treatment with higher concentrations of malonic acid lowered the rate of O_2 absorption only by an additional 9 per cent. over that at 0·01 M concentration. It is possible that in this tissue some kind of tissue resistance may have set in to stop the further progress of the inhibitor.

(2) *Effect of malonic acid on the CO_2 evolution of tissues.*—The trend of CO_2 evolution also presented interesting variations both from tissue to tissue as well as from treatment to treatment. The rate of CO_2 evolution varied from 42·7 to 121·2 c.mm. in the different tissues, exhibiting similar fluctuations as in O_2 absorption. Just as in O_2 absorption some tissues exhibited an increased rate of CO_2 evolution with malonic acid treatment while all the tissues investigated showed inhibition in CO_2 output with lower or higher concentrations of malonic acid feeding. The data collected with respect to CO_2 output are presented in Table I and Text-Fig. 1.

In *Ananas sativa* and *Pitcairnia* sp., acceleration of CO_2 output was observed in the lower concentrations of malonic acid up to 0·02 M and thence a reduction in CO_2 output with further increase in malonic acid concentration. In the highest concentration (0·05 M) used the percentages of inhibition in these plants were 48·2 and 37·5 respectively.

In *Begonia anamalayana* malonic acid feeding brought about a gradual decline in the rate of CO_2 evolution. In *Billbergia* sp., however, considerable fluctuations were observed at the different concentrations, but in general there was a slight depression in CO_2 evolution. In *Kalanchoe* sp., 0·01 M malonic acid treatment resulted in a sudden fall (42·1 per cent.) in CO_2 and in the higher concentrations a further depression was observed though with slight fluctuations. Similar features were also observed in *Bryophyllum calycinum*, except at 0·01M where a slight increase over the control was observed. The inhibiting effect of malonic acid on CO_2 evolution in *Bryophyllum tubuliformis* was stronger than in any other plant species studied here. With increase in the concentration of malonic acid, the low CO_2 rate observed at 0·01 M was almost maintained throughout. In *Bryophyllum* sp., the response to the inhibitor, was different from the other tissues as the CO_2 evolution at 0·01 M showed a slight increase (19·5 per cent.) over the control. Further increases in the malonic acid concentration resulted in a depression in CO_2 evolution.

(3) *Effect of succinic acid on malonic acid-treated tissues.*—It has been suggested by a number of workers (Hopkins *et al.*, 1938; Krebs and Eggleston, 1940 and Potter and Dubois, 1943) that malonate inhibits succinic dehydrogenase probably by forming a dissociable

complex with succinic dehydrogenase resulting in the blocking of the Krebs TCA-cycle at the succinic acid link. It has also been suggested that malonate may inhibit the reaction, through its competitive action on succinic dehydrogenase. In the latter case it should be possible to obtain reversal of the inhibition by the addition of a further quantity of succinic acid. Apart from the reversibility of the inhibition with malonic acid, there is another feature, namely, acceleration with malonic acid treatment. To verify all these possibilities, tissues treated with 0·04 M malonic acid have been used, where the maximum amount of inhibition in a number of tissues and also some amount of acceleration in some tissues were observed in the previous experiments. Two concentrations of succinic acid were tried, namely, 0·0125 M and 0·025 M along with 0·04 M malonic acid to study the gaseous exchanges in both the types of tissues—those that were stimulated as well as those that were inhibited by malonic acid.

The data collected in these experiments are presented in Table II and Text-Fig. 2. Further rise in O_2 absorption was observed in plants where there was stimulation with malonic acid treatment. Reversibility of the inhibition was obtained in all the other inhibited plants, except in *Billbergia* sp. and *Bryophyllum tubuliformis* where the values were very much reduced with the succinic acid treatment. But complete recovery to the control level was obtained only in *Bryophyllum calycinum*. Thus from the data collected on the effect of succinic acid on malonic acid-treated tissues the plants studied in these investigations may be divided into four groups.

Group I

Ananas sativa and *Pitcairnia* sp. in which malonic acid brought about an increased O_2 absorption, CO_2 evolution and addition of succinic acid enhancing these values still further.

Group II

Billbergia sp. and *Bryophyllum tubuliformis* in which malonic acid inhibited the rate of gaseous exchange and addition of succinic acid failing to bring about any reversal.

Group III

Kalanchoe sp., *Bryophyllum* sp. and *Begonia anamalayana* in which malonic acid produced an inhibition and in which addition of succinic acid reversed the inhibition only to a slight degree for the reversal values did not reach those of the control.

Group IV

Bryophyllum calycinum in which also malonic acid inhibited respiration and where also succinic acid brought about a reversal of this inhibition, but here the reversal was complete and the succinic acid-treated sets gave oxygen absorption values as high as or higher than the control.

TABLE II

Effect of succinic acid on malonic acid-treated tissues

Name of the plant	Treatment to the tissue	C.mm. of O_2 absorbed G.F.Wt./ Hr.	% of recovery over inhibited tissue	C.mm. of CO_2 evolved G.F.Wt./ Hr.	% of recovery over inhibited tissue
Ananas sativa	Control	48·5	..	65·1	..
	0·04 M Malonic acid	52·1	..	55·7	..
	0·04 M Malonic acid 0·0125 M Succinic acid	110·8	110·8	120·0	115·3
	0·04 M Malonic acid 0·025 M Succinic acid	92·4	77·4	117·6	111·1
Pitcairnia sp.	Control	33·7	..	42·7	..
	0·04 M Malonic acid	35·0	..	63·7	..
	0·04 M Malonic acid 0·0125 M Succinic acid	44·0	25·7	90·0	42·9
	0·04 M Malonic acid 0·025 M Succinic acid	39·6	11·7	52·4	0
Begonia anamalayana	Control	51·6	..	83·3	..
	0·04 M Malonic acid	30·5	..	50·9	..
	0·04 M Malonic acid 0·0125 M Succinic acid	44·0	11·4	62·4	22·6
	0·04 M Malonic acid 0·025 M Succinic acid	46·4	12·1	69·6	36·7
Billbergia sp.	Control	63·6	..	77·3	..
	0·04 M Malonic acid	41·5	..	69·6	..
	0·04 M Malonic acid 0·0125 M Succinic acid	15·6	0	20·8	0
	0·04 M Malonic acid 0·025 M Succinic acid	24·4	0	33·6	0

TABLE II (*Contd.*)

Name of the plant	Treatment to the tissue	C. mm. of O_2 absorbed/ G.F.Wt./ Hr.	% of recovery over inhibited tissue	C. mm. of CO_2 evolved G.F.Wt./ Hr.	% of redovery over inhibited tissue
Kalanchoe sp.	Control	65·2	..	81·7	..
	0·04 M Malonic acid	20·7	..	29·2	..
	0·04 M Malonic acid 0·0125 M Succinic acid	24·4	17·9	30·8	5·4
	0·04 M Malonic acid 0·025 M Succinic acid	24·4	17·9	33·6	15·1
Bryophyllum calycinum	Control	88·0	..	121·2	..
	0·04 M Malonic acid	35·0	..	81·3	..
	0·04 M Malonic acid 0·0125 M Succinic acid	72·8	108·0	96·8	19·1
	0·04 M Malonic acid 0·025 M Succinic acid	96·8	176·6	122·4	50·6
Bryophyllum tubuliformis	Control	69·5	..	115·7	..
	0·04 M Malonic acid	21·0	..	29·9	..
	0·04 M Malonic acid 0·0125 M Succinic acid	8·8	0	15·2	0
	0·04 M Malonic acid 0·025 M Succinic acid	15·6	0	27·6	0
Bryophyllum sp.	Control	66·3	..	68·9	..
	0·04 M Malonic acid	28·8	..	68·8	..
	0·04 M Malonic acid 0·0125 M Succinic acid	42·0	45·8	56·8	0
	0·04 M Malonic acid 0·025 M Succinic acid	46·4	61·1	64·4	0

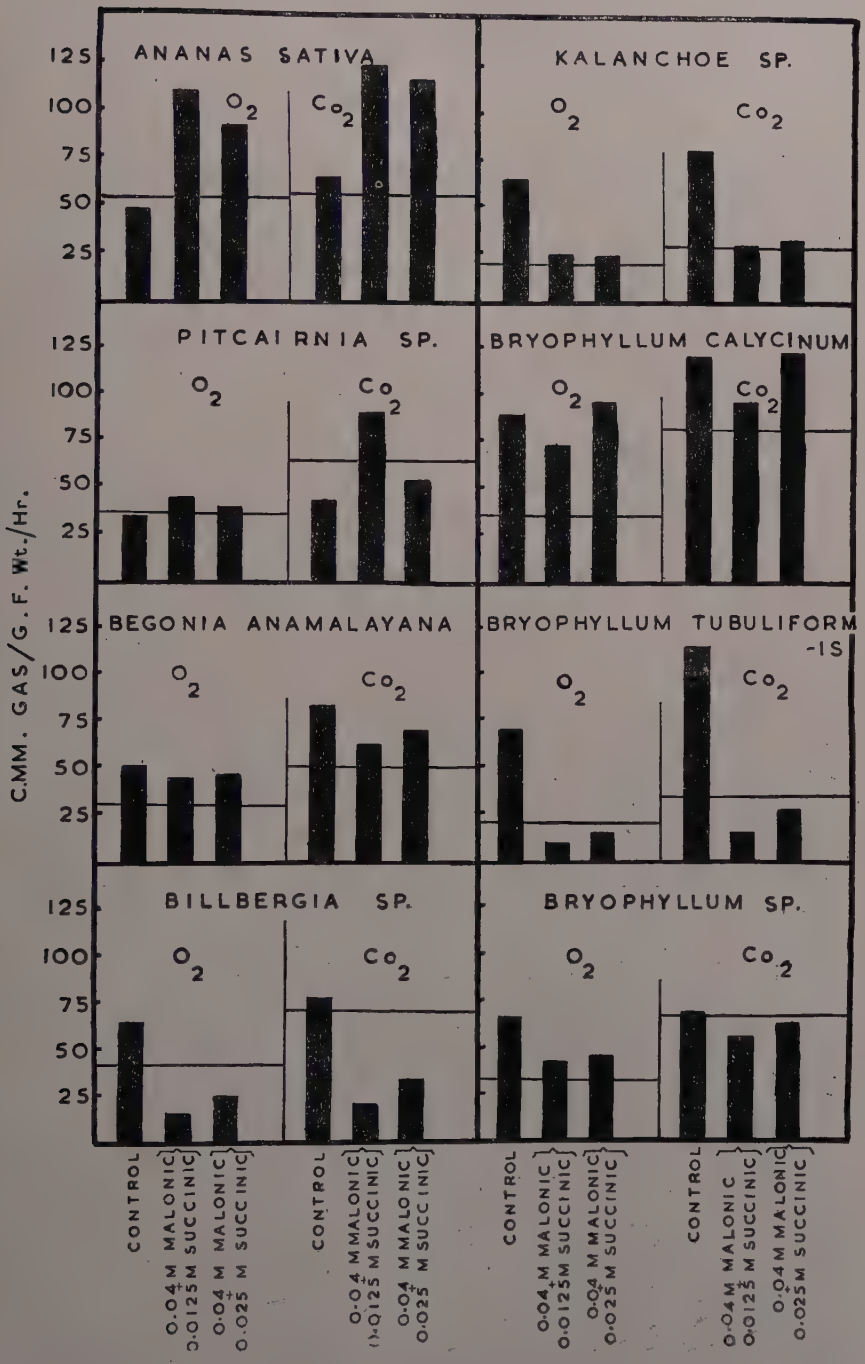

ANANAS SATIVA
KALANCHOE SP.
PITCAIRNIA SP.
BRYOPHYLLUM CALYCINUM
BEGONIA ANAMALAYANA
BRYOPHYLLUM TUBULIFORM -IS
BILLBERGIA SP.
BRYOPHYLLUM SP.
O2
Co2
125
100
75
50
25
C.MM. GAS/G. F. Wt./Hr.
CONTROL
0·04 M MALONIC
0·0125 M SUCCINIC
0·04 M MALONIC
0·025 M SUCCINIC

FIG. 2

TEXT-FIG. 2. The effect of the addition of succinic acid on the gaseous exchange of tissue slices pre-treated with 0·04 M malonic acid. Horizontal lines are the values obtained for tissues treated with 0·04 M malonic acid.

DISCUSSION

It is evident from the data presented above that malonic acid inhibits O_2 absorption and CO_2 evolution in some tissues and accelerates the gaseous exchanges in the other tissues studied. In such of those tissues where there is inhibition, feeding with succinic acid reverses this effect in some tissues to a slight or considerable extent. Malonic acid is known to inhibit the action of succinic dehydrogenase (Quastel and Whetham, 1925) and it has been suggested that malonic acid combines with succinic dehydrogenase to form a dissociable complex and the series of reactions of the Krebs TCA-cycle are interrupted at this stage.

It may be observed from Table III that of the six molecules of O_2 absorbed only four molecules are absorbed up to the stage of reaction in which succinic dehydrogenase takes part and the remaining two molecules are not absorbed if the other two reactions after succinic acid formation in the Krebs cycle do not occur. Thus the inhibitive action of malonic acid, if it affects the cycle at the succinic dehydrogenase stage should result in an inhibition of $\frac{1}{3}$ normal O_2 uptake. In most of the tissues studied in these investigations (Table I, Text-Fig. 1) except *Kalanchoe* sp. and *Bryophyllum tubuliformis*, the values for inhibition of O_2 absorption range from 30 to 40 per cent. in low concentrations of malonic acid. It may be inferred from this that in these tissues the inhibition of O_2 absorption is through the effect of malonic acid on succinic dehydrogenase. The high values of inhibition of oxygen absorption in *Kalanchœ* sp. and *Bryophyllum tubuliformis* and in a few other tissues where very high concentrations of malonic acid used resulted in inhibitions above 40 per cent., are possibly due to the effect of malonic acid on some other enzymes of the Krebs cycle, thus possibly interrupting the cycle even in an earlier stage. Evidence on this has been obtained by some earlier workers (Das, 1937; Pardee and Potter, 1949).

It has also been suggested that malonic acid inhibits O_2 absorption through its competitive action on succinic dehydrogenase (Hopkins, *et al.*; Krebs and Eggleston, 1940 and Potter and Dubois, 1943). In such a case it should be possible to obtain a reversal of the inhibition by the addition of succinic acid. Data obtained in these investigations show that in *Kalanchoe* sp., *Begonia anamalayana*, *Bryophyllum* sp. and *Bryophyllum calycinum* there is partial or complete reversal of this malonic acid inhibition. These features suggest that malonic acid probably acts competitively on succinic dehydrogenase and when the concentration of succinic acid is sufficiently high there is a reversal of this inhibition. Where the reversal is only partial it may be that malonic acid acts on other enzymes of the Krebs cycle also. Further work now being planned in this laboratory, to find out

TABLE III

Reactions involving, for continuous operation, the uptake of one molecule of oxygen (from Thomas, 1956)

Substrate (Two molecules consumed)	Type of reaction	Intermediate hydrogen carrier	Estimated P/O value
Triosephosphate ..	Dehydrogenation	DPN	8
Pyruvate ..	Oxidative decarboxylation	DPN	8
Isocitrate ..	Dehydrogenation	TPN	6
Ketoglutarate ..	Oxidative decarboxylation	DPN	8
Succinate ..	Dehydrogenation	Cyt. c.	4
Malate ..	Dehydrogenation	TPN or DPN	6

the effect of other acids of the Krebs cycle on these tissues, treated with malonic acid, should throw further light on this point.

Another interesting feature of the effect of malonic acid on O_2 absorption is the augmenting effect observed in *Ananas sativa*, *Pitcairnia* sp. and to a slight extent in *Begonia anamalayana* (Table I, Text-Fig. 1). In these tissues feeding malonic acid even in low concentrations resulted in considerable increases in O_2 absorption. Such an accelerating effect has been reported by Burris and Wilson (1939) in *Rhizobium*. Albaum and Eichel (1943) in Coleoptiles of *Avena* and by Eny (1952) in *Chlorella*. It was Gray (1952) who suggested for the first time a possible mechanism, when he observed that *Pseudomonas aeruginosa* decarboxylated malonic acid to give acetic acid. Besides other evidences, a recent report by Giovanelli and Stumpf (1957) is of great interest. They obtained evidence from their work on peanut mitochondria, suggesting the position of malonate in metabolism by the following scheme:

$$\text{Malonate} \xrightarrow{\text{ATP; CoA}} \text{Malonyl Co A} \rightarrow CO_2 + \text{Acetyl Co A} \rightarrow \text{Krebs cycle.}$$

The increasing effect on oxygen absorption of low concentrations of malonic acid in some of the tissues in the present investigations clearly shows that a reaction of the type suggested by Giovanelli and Stumpf

(*loc. cit.*) is taking place and malonic acid is also consumed as a metabolite in these tissues. The increases in CO_2 output observed in these tissues may thus be due to its liberation in the decarboxylation of malonic acid as suggested above.

It may be further observed that addition of succinic acid to malonic acid-treated *Ananas sativa* and *Pitcairnia* tissues resulted in a higher rate of oxygen absorption to a level higher than the malonic acid-treated tissues. Obviously in these tissues increased succinic acid feeding hastens that part of the cycle after the succinic acid stage.

It may thus be seen that malonic acid may act not only as an inhibitor of succinic dehydrogenase but also as an inhibitor of other enzymes of the Krebs cycle. It may also serve as a metabolite in some tissues and hence due care has to be taken in interpreting data obtained with malonic acid treatments.

Summary

Effect of malonic acid in different concentrations on O_2 absorption and CO_2 output in leaves of *Ananas sativa*, *Pitcairnia* sp., *Begonia anamalayana*, *Billbergia* sp., *Kalanchoe* sp., *Bryophyllum calycinum*, *Bryophyllum tubuliformis* and *Bryophyllum* sp., have been studied.

In general in *Billbergia* sp., *Kalanchoe* sp., *Bryophyllum calycinum*, *Bryophyllum tubuliformis* and *Bryophyllum* sp., malonic acid treatment resulted in an inhibition of O_2 uptake, the inhibition ranging between 22·5 to 76·9 per cent. at the higher concentrations studied. It has been suggested that where the inhibition was of the order of about 30 per cent. malonic acid probably inhibits succinic dehydrogenase action by successfully competing with succinic acid. Where the inhibitions are of higher order it is possible that malonic acid affects some other enzymes of the Krebs cycle blocking the pathway at an earlier stage.

In *Ananas sativa*, *Pitcairnia* sp. and *Begonia anamalayana*, there was an acceleration in O_2 absorption. This is believed to be due to the fact that malonic acid is used as a metabolite in these tissues according to the following scheme suggested by Giovanelli and Stumpf:

$$\text{Malonate} \xrightarrow{\text{ATP, Co A}} \text{Malonyl Co A} \rightarrow CO_2 + \text{Acetyl Co A} \rightarrow \text{Krebs cycle.}$$

CO_2 evolution followed the same trend as O_2 absorption in malonic acid-treated tissues though the fluctuations were not so marked.

To test the reversibility of malonic acid inhibition, the treated tissues have been fed with succinic acid and reversibility was obtained in a large number of cases. This confirms the view that malonate acts in a competitive way on succinic dehydrogenase.

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THE DISTRIBUTION AND ROLE OF SUCROSE IN PLANTS

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Introduction

Since publishing my paper on the Sugars of the Snowdrop Leaf (Parkin, 1912) I have endeavoured to keep pace with the literature dealing with the part played by carbohydrates in the metabolism of living organisms, being particularly concerned with the distribution and rôle of sucrose in the plant kingdom. The majority of such researches which have come within my knowledge have strengthened my belief in the fundamental importance of this sugar. In fact this disaccharide seems to be the sugar *par excellence* for the green (chlorophyll-containing) plant from the Algæ upwards.

If this be granted then the question arises why is this so? Particularly as in the sister kingdom, the Animal, sucrose would appear to be entirely absent. The monosaccharide, *d*-glucose, is here undoubtedly the sugar of prime importance.

Up to the publication of Brown and Morris's classical paper on the Chemistry and Physiology of Foliage Leaves (1893) sucrose might be said to have been generally regarded as an easily convertible *reserve* carbohydrate. Brown and Morris, however, from their investigations of the carbohydrates of the *Tropæolum* leaf (the common nasturtium of our gardens) came to the unexpected conclusion that sucrose, rather than a hexose sugar, should be regarded as the first sugar to be set free in photosynthesis. Previously the well-known researches of Sachs pointed to starch as the first visible product of carbon assimilation. But it was generally conceded that some sugar must precede the appearance of starch. This was usually considered to be glucose, as starch when completely hydrolysed yields only this monosaccharide. Hence Brown and Morris's view came as distinctly novel and has been the subject of controversy ever since though quite recently (Calvin, 1955) it looks as if their contention appears to be justified.

The Chemistry of Sucrose

Before proceeding it may be of interest to dwell a little on the chemistry of this disaccharide—particularly as for long it resisted synthesis *in vitro* after many attempts. The most noticeable historically was that by Pictet and Vogel (1928). They claimed to have synthesized sucrose by purely chemical means. This claim failed to be

justified by subsequent investigators and what appears to have been obtained was a small quantity of an isomer of this sugar now termed iso-sucrose.

Up to 1952 the cry of despair in carbohydrate chemistry was the resistance of sucrose to its synthesis *in vitro*. Then in this year the accomplishment of this was announced before the American Chemical Society and was deemed so important that even the daily press commented on it ! (see *Daily Telegraph*, September 8th, 1952). Lemieux and Huber (1953) were the successful scientists working together in a Canadian laboratory. They heated together tri-*o*-acetyl-D glucosan and tetra-*o*-acetyl-D fructofuranose in a sealed tube at 100° for 104 hours. Sucrose octa-acetate was obtained and this on deacetylation yielded a small amount of crystalline sucrose giving a melting-point of 187°. But such a synthesis is far removed from what the plant can accomplish with ease at a normal temperature and in quantity too. So the press need not imagine cane sugar being supplied in quantity by purely chemical means to supplement our sugar supply from natural sources ! What the biochemist may accomplish in the future by means of enzymic and such-like action is another matter. The capability of the bacterium, *Pseudomonas saccharophila*, of synthesizing sucrose from a mixture of fructose and glucose phosphate would seem to point the way (Hassid *et al.*, 1944).

The atoms in the sugar molecule used to be represented graphically as arranged in chains, but for the last 30 years or so, thanks to the researches of Haworth and others, it has been shown that such atoms are really joined in rings. Further, it was shown that these rings could be of two kinds—either 6-membered termed pyranose or 5-membered termed furanose—the latter often referred to for brevity's sake as the γ-form.

Sucrose before its chemical synthesis had upon reactive evidence been proved to have the glucose half of its molecule in the pyranose and the fructose half in the furanose form. Further, of the two isomeric forms, α and β, capable of existing, it was shown later that the glucose component is in the former state and the fructose in the latter, so the formula of sucrose can be written as

α-D-glucopyranosyl-β-D-fructofuranoside.

Further, it has been shown that whenever fructose occurs in combination with itself to form polysaccharides, such as inulin and fructosans generally, it is in the furanose, whereas glucose under similar conditions is in the pyranose state.

Another important point is that when fructose is set free from combination by hydrolysis it changes at once from the furanose to the pyranose state. Hence it may be concluded that fructose furanose, the γ-form, cannot as far as we know be obtained in the free state; but derivatives of fructofuranose, such as phosphatic esters, can be readily produced in the course of simple chemical reactions.

Further, Professor E. L. Hirst has pointed out to me a really greater difficulty in its synthesis *in vitro* than that of its two components being in different ring formation. This is the combining of the α-form of pyranose glucose with the β-form of furanose fructose. It is very much easier to prepare by chemical methods β than α glucosides.

Thus sucrose has two marked features in its molecule, namely, the two hexose residues in different ring forms and the α glucose combined with the β fructose.

It is interesting also to point out that sucrose, unlike the disaccharide maltose, is non-reducing and cannot therefore be estimated directly by the copper (Fehling's) method. It has long been known to break down on hydrolysis by acid or by the enzyme invertase (sucrose) into equal parts of the monosaccharides D-glucose and D-fructose. This is often spoken of as inversion on account of the plane of polarised light changing from the *plus* to the *minus* side—a ready means of estimating the percentage of sucrose in a mixture.

Unlike maltose sucrose does not form an osazone.

Distribution of Sucrose

Sucrose is peculiar to the plant kingdom. As far as we know it has never been found in animals. As soon as it is taken in as food by the animal body it is inverted into its two hexose constituents. The only disaccharide—at any rate of importance as far as we know—occurring in animals is the lactose of milk. Superficially viewed this strikes one as odd for it brings into its composition galactose—a hexose apparently of less intrinsic value than either glucose or fructose and one of comparatively rare occurrence in the free state in either kingdom.

As glucose is the travelling form of sugar in the animal body one assumes that carbohydrate reaches the mammary gland as such. Presumably part of the glucose is converted into galactose and the two combine to form the disaccharide lactose. How this is brought about is, I fancy, not yet at all clear. Perhaps some form of phosphorylation, coupled with enzymic action, is involved. The synthesis is not so straightforward as one might expect. For it has been shown that when thin slices of active mammary tissue are incubated with a mixture of glucose and galactose it is only the former hexose that is utilised in lactose synthesis.

Why lactose should have been selected as the nutritive carbohydrate of milk is an interesting problem. Unlike sucrose, lactose is a reducing sugar. It is also less sweet and is not fermentable by ordinary yeasts. Regarding the matter from a stark utilitarian point of view, one would have thought the condensation of glucose directly to a disaccharide containing two combined glucose residues would have been a simpler synthesis producing maltose or a disaccharide akin, but this is not so. The same reasoning is applicable to reserve carbohydrates in seeds and other storage organs in plants. Carbohydrate

metabolism *in vivo* is at present so much ahead and easier of accomplishment to what we can as yet bring about *in vitro*.

But I am digressing, suffice it to say that the way lactose is formed from glucose in the mammary gland may have a bearing on the way glucose is converted into sucrose in the plant.

Though sucrose is widespread in plants it is not universal in this kingdom. For instance it appears to be absent in Fungi and its place may be held to be taken by the disaccharide, trehalose. Hence the distribution of sucrose among plants is a matter of considerable interest and possibly allows of a certain amount of speculation.

Angiosperms.—It may be taken for granted that sucrose is generally present in Angiosperms (Flowering Plants). Schulze and Frankfurt (1895) showed years ago how widely it was spread here. Recently using paper chromatography, Bidwell *et al.* (1952) found sucrose present in 27 families of Spermatophyta examined and still more recently Norris *et al.* (1955) in a cross-section of Angiosperms find sucrose present in a representative of the following families,—Lauraceæ, Leguminosæ, Cucurbitaceæ, Crassulaceæ, Araliaceæ, Solanaceæ and Gramineæ.

To pursue the spread of sucrose further in flowering plants would be merely to labour the matter, better to consider instances of the reported absence of sucrose. In such cases one has to bear in mind the possibility of its undergoing inversion during manipulation of the material for examination. It is a sugar very easily hydrolysed by acidic or enzymic action. The new technique of paper chromatography is invaluable here as expressed sap can be immediately subject to the separation of its sugars before much alteration can have taken place.

In this connexion the genus *Gentiana* might be worth investigation as regards the sugars in its foliage leaves. Kylin (1918) points to the absence of sucrose in the leaves of *Gentiana brevidens* suggesting that this sugar may be replaced by another. Previous to this Bridel (1911) found that the root of *Gentiana lutea* contained, besides glucose, fructose and sucrose, another sugar gentianose. It is therefore possible that the gentian leaf accumulates gentianose rather than sucrose.

Gentianose is a trisaccharide consisting of the condensation of two molecules of glucose with one of fructose. Emulsin can split it into sucrose and glucose. It is thus somewhat akin to raffinose which by the same enzyme gives sucrose and galactose. Hence a more detailed investigation of the sugars in the gentian leaf by modern methods would seem desirable.

Angiospermous plants which might be of interest as regards their carbohydrate metabolism are ones lacking green colouring. Here are a few parasitic and saprophytic plants devoid for the most part of chloroplasts in their leaves. I am unaware of their having been investigated. Among parasitic ones one might mention the too thwort (*Lathræa squamaria*) and the broomrapes (*Orobanche*) and among the saprophytes some of the orchids such as the bird's-nest orchid (*Neottia*

nidus-avis). If cane-sugar is present in these it cannot well have arisen directly through photosynthesis since chloroplasts are mainly if not wholely absent. It may have been obtained directly from the host or humus or else synthesized by the plant itself.

Gymnosperms.—Though the flowering plants have been mainly studied as regards their carbohydrates such investigations that have included Gymnosperms have shown the presence of sucrose in them.

Lefebvre (1907) found it in the twigs of the yew (*Taxus baccata*) along with raffinose, Schulze and Godet (1909) in seeds of species of *Pinus* and *Picea*, Hatorri and Shiroya (1951) in seeds and seedlings of *Pinus thunbergii*. Quite recently Norris *et al.* (*l.c.*) find sucrose in considerable quantities in yew and juniper.

As far as I am aware the Gnetales, cycads and *Ginkgo* have not had their carbohydrates investigated.

Pteridophyta.—Ferns have been little studied as regards their sugars, but there can be little doubt that sucrose is generally distributed in them. Norris *et al.* (*l.c.*) found it in considerable quantities in *Ceratopteris* and *Polystichum*.

The lycopods, *Equisetum*, etc., have likewise received little attention; but Bourquelot (1903) found *Selaginella denticulata* an exception in 57 plants of various affinities examined in not containing sucrose. This result wants confirming or more likely modifying under modern technique.

Bryophyta.—Though mosses and liverworts have been little studied as regards their carbohydrates, when they have been so sucrose has been found markedly present. Goris and Vischniac (1913) definitely proved the presence of sucrose in the mosses *Sphagnum cymbifolium* and *Hypnum purum*. A little later Mason (1916) found sucrose plentiful also in species of *Sphagnum* as well as in *Thuidium tamariscinum* and *Polytrichum commune*. Since then Norris *et al.* proved sucrose in abundance in *Funaria* (Protonemata) and *Fontinalis* (mature gametophyte).

The liverworts (Hepaticæ) have escaped examination until very recently. Norris *et al.* included in their cross-section one liverwort (mature gametophyte) and found sucrose present in considerable quantity.

Algæ.—Until fairly recently the presence of sucrose in this vast phylum of plants had not been definitely proved. Some years ago Parkin (1925) wrote that "the point of entry of cane-sugar in the evolution of the plant kingdom may thus be of some importance. A thorough investigation of the Algæ might solve the problem". Now thanks to the Calvin School and others it looks as if sucrose is generally present, though further research here is badly needed. Quite recently doubt has been cast on the presence of sucrose in some Brown and Red Algæ tested. This will be discussed later in this review.

The Algæ can conveniently be divided into main groups of distinctive colouring which corresponds fairly closely with other points of difference. The colours are green (Chlorophyceæ), yellow-green (Xanthophyceæ), brown (Phæophyceæ), red (Rhodophyceæ) and blue-green (Myxophyceæ). Besides these Fritsch (1935 and 1952) in his monumental and indispensable text-book adds six more classes including one composed of diatoms and the others of small compass,—the most striking of these being the Euglenineæ, highly specialised and of considerable interest from the view-point of nutrition.

It is generally conceded that the higher plants most probably arose from some past members of the Chlorophyceæ. Their chlorophyll is very similar and their carbohydrate reserve is usually starch, further the cell-wall is largely cellulose. What we know at present as regards the sugars of the Chlorophyceæ suggests that sucrose may be generally present. The Calvin School (Norris *et al.*, *l.c.*) in their recent survey of chlorophyll-containing plants find sucrose present in the following Green Algæ, *Chlorella*, *Chlorococcum*, *Nitella*, *Scenedesmus*, *Spirogyra* and *Vaucheria*, but almost no sugar at all in *Haematococcus* (*Sphaerella*).

As regards the Xanthophyceæ (Heterokontæ) the genus *Vaucheria*, included as above in the Chlorophyceæ, should now be placed here as recently its paired cilia have definitely been shown by the electron microscope to be unequal, *i.e.*, heterokont (Greenwood *et al.*, 1957). Besides it stores oil instead of starch—a characteristic of the yellow-green Algæ. So that one can say that sucrose has been found present in Xanthophyceæ.

The Phæophyceæ—a very large marine group—has with little doubt evolved mainly on its own and has no obvious affinities with other algal classes though they have certain points in common with the Xanthophyceæ. Unfortunately Norris *et al.* (*l.c.*) did not include a member of this class. However, Bidwell *et al.* (*l.c.*) did include three species in their chromatographic study of sugars in plants and found very small, but recognisable amounts of sucrose in two of these. In these seaweeds instead of starch a reserve polysaccharide akin to it known as laminarin is generally present. It hydrolyses like starch completely to glucose.

Another very large, mainly marine group of Algæ, the Rhodophyceæ, has likewise no obvious relationship with any other unless it be with the Myxophyceæ on account of a similarity in their additional pigments—more likely only a parallelism. Just one red alga, a species of *Porphyridium*, was included in the Norris *et al.*, cross-section and a small amount of sucrose was indicated. A polysaccharide spoken of as Floridean starch occurs abundantly in the Rhodophyceæ and may be regarded as a condensed product of carbohydrate photosynthesis taking the place of ordinary starch. It stains to some extent with iodine and has perhaps a chemical affinity with glycogen.

The blue-green Algæ, the Myxophyceæ (Cyanophyceæ) are usually regarded as the lowest, least evolved, group as they lack sexual organs and their chlorophyll is not segregated into definite chromatophores.

Also the cell nucleus is not well defined. Sucrose has been recognised by the Calvin School (Norris *et al.*, *l.c.*) in three of the four species examined, namely, two *Nostoc* and one *Phormidium*. The other member of the group examined, *Synechococcus*, revealed no sugar of any kind. The reserve carbohydrate of these algæ appears to be more of the nature of glycogen than starch.

Reviewing the carbohydrate content of the Algæ as a whole the amount of free sugar present is considerably less than in the higher plants. For example, taking the Bryophyta as the lowest group of the higher plants the average for sucrose of the three plants examined by the Calvin School gives the comparative figure of 38·5, whereas the average of the six green Algæ (Chlorophyceæ) comes only to 4·8 with *Spirogyra* the highest at 9·9. They suggest that the marked difference may be correlated with the amount of non-photosynthetic tissue present. When this is absent or only in small quantity, the sucrose presumably formed in photosynthesis has no place in which to store itself temporarily and so the surplus is condensed at once into polysaccharide reserve or utilised in growth. This seems an interesting point to be followed up in the higher plants. Does something of the kind occur in Monocotyledons which on the whole appear to hold more free sugar—largely sucrose—in their tissues then Dicotyledons? The latter are the greater starch-formers. This is discussed more fully later in the review.

Bacteria.—Though we do not usually think of bacteria as photosynthetic organisms, yet there are some interesting forms which assimilate CO_2 by means of light using H_2S as donor instead of H_2O as is general for green plants. These are the purple and green sulphur bacteria. They contain a photosynthetic pigment similar to chlorophyll *a* with slight differences.

So far these bacteria seem to have been passed over as regards their carbohydrates. It would be interesting to see whether sucrose could be detected in them after exposure to light. Further remarks on these species and on bacteria generally are reserved for the discussion.

Lichens.—The sugars of these symbiotic plants have been little studied. More attention has been paid to the polysaccharide reserves such as lichenin which produce glucose on hydrolysis. But sucrose has been detected (Lindberg and Wickberg, 1953). Most likely the sucrose has arisen through the algal symbiont. Trehalose also occurs in lichens and this sugar looks as if coming from the fungal side.

The presence of sucrose in lichens and not in fungi raises the interesting question as to whether sucrose can be detected in those animals which incorporate into their bodies green alga-like cells, *e.g.*, *Hydra viridis* (the common freshwater *Hydra*) and the marine worms, *Convoluta*, investigated by Keeble (1910). He refers to the green cells of *Convoluta roscoffensis* as capable of photosynthesis and storing starch.

The Role of Sucrose

Having taken a general, though perhaps a somewhat cursory, survey of the distribution of sucrose in the plant kingdom one now turns to

the part this sugar plays as far as we know in the green plant's metabolism. At the outset we have to consider how it arises and this brings us to the vexed question as to how it is set free in photosynthesis.

The First Sugar of Photosynthesis.—Ever since Brown and Morris (1893) put forward the unexpected idea at that time that sucrose and not glucose is the first sugar to be set free in photosynthesis the matter has been keenly debated.

They were not as it happens the first to put forward the sucrose view. Eleven years earlier Perry (1882) in studying the carbohydrates in the leaves of the haricot bean (*Phaseolus*) concluded that "le sucre de canne est un produit de l'élaboration directe de la cellule verte" finding glucose absent. Brown and Morris were perhaps unaware of this paper as it is not mentioned in the text or in their list of references. Also the work of Girard (1884) on the sugar-beet a year later escaped their notice. This investigator was of the opinion that sucrose is formed in the leaf by direct photosynthesis. These papers evidently made no marked impression at the time.

It is unnecessary to enlarge in detail on the controversy respecting the first sugar of photosynthesis, let it suffice to mention a few of the more important researches bearing on this point. On the one hand the sucrose view was favoured by Went (1898), Parkin (1912 on the snowdrop), Davis *et al.* (1916 on the mangold and potato) and Gast (1917); while on the other hand the glucose view was clung to by Campbell (1912 on the mangold), Weevers (1924), Clements (1930) and Barton-Wright and Pratt (1930 on *Narcissus*).

Why the sucrose view appeared to be so difficult of acceptance may be attributed to the Baeyer (aldehyde) theory of photosynthesis being still prevalent in the minds of botanists.

Since then the Baeyer hypothesis—simple though it was—has had to be discarded, particularly as the whole aspect of carbon assimilation had in the meantime undergone radical change, the oxygen evolved being no longer considered as coming from the carbon dioxide but rather from the water. Hence the way carbohydrate is set free in photosynthesis had to be sought for elsewhere.

The elaborate investigations of the Calvin School (Calvin, 1956), using radioactive carbon dioxide ($C^{14}O_2$) for spotting and paper chromatography for the identification of the photosynthetic products, point strongly to sucrose as being the first sugar to be liberated. Phosphorus is the magic element taken into combination leading eventually to a composite ester of glucose and fructose phosphates joined together. On the elimination of the phosphate sucrose is set free. This is putting the matter simply. The photosynthetic carbon cycle appears to be very complicated, but the main outcome from the carbohydrate standpoint would seem to be the production of free sucrose for general purposes.

The Glucose-Fructose Ratio.—From the time of Brown and Morris' classical work on the carbohydrates of the *Tropæolum* leaf attempts have

been made to estimate separately these two hexoses in foliage leaves. These monosaccharides are the only ones we know to exist in any quantity in the free state. The other two hexoses, mannose and galactose, never seem to accumulate in the simple form, though they exist frequently in seeds and other reserve organs as polysaccharides—often mixed with pentosans.

Brown and Morris's figures for the glucose-fructose ratio can only have a small quantitative significance. Any quantitative deduction to be drawn from them is vitiated by the method of estimation used, which must have resulted in much destruction of the fructose by the hydrochloric acid used in hydrolysing the maltose. It is astonishing then to find such high figures for the fructose. Parkin's problem with the snowdrop was less difficult as he had not to deal with the estimation of maltose. His figures suggest little difference between the amounts of the two hexoses, though on the whole favouring an excess of fructose.

Davis (1916) in his valuable paper on this ratio using the mangold leaf points out that as the estimations of the two hexoses are based on the polarimetric readings these may be invalidated by the presence of optically active substances other than sugars such as amides or amino-acids not wholly removed by the agents (basic lead acetate as a rule) used to clear the solutions. It is here that he particularly criticises Parkin's results. After yeast fermentation Parkin found his solutions gave no appreciable rotatory and reducing power and so concluded that no substances besides sugars were present in the original solution. But Davis points out that asparagine for example might have been present but consumed by the yeast in its growth during fermentation. Davis therefore sums up as follows: "It is impossible in the present state of our knowldge to draw any conclusions from the proportion of apparent dextrose or lævulose [glucose or fructose] in plant tissues as to whether either of these sugars is better adapted than the other to tissue formation or to respiration. All such conclusions in the past are valueless because the analytical methods at present existing do not give true values for these sugars." Barton-Wright and Pratt (1930, p. 1222) wisely did not attempt to give separate figures for these two sugars, lumping them together as hexose sugar.

Now with the new technique of paper chromatography and labelled carbon this ratio might be re-studied with more certainty.

Sucrose-Hexose Ratio.—Parkin found in the snowdrop leaf little variation in the amount of hexose sugar during the 24 hours, whereas the sucrose fluctuated greatly increasing by day and decreasing by night, the inference being that a small amount of sucrose was continually being inverted to supply sugar for respiration—the main bulk of the sucrose being conducted away for storage purposes. Later investigations have not altogether given figures supporting this view. In fact Davis *et al.* (1916) as regards mangold leaves conclude from their figures that the fluctuations of the hexoses during the 24 hours is far greater than of he saccharose (sucrose). Barton and Wright's figures (Barton-Wright

and Pratt, 1930) for the *Narcissus* leaf supports to some extent Parkin's deduction.

More recently Guichard (1954) in his investigation of the sugars of the vine finds little change in the amount of hexose in the leaves during 24 hours in contrast to sucrose thus supporting Parkin's figures for the snowdrop.

In this connexion might be mentioned the fact that as the leaf ages the proportion of hexose sugar to sucrose is inclined to increase. This would appear to be so for the snowdrop, mangold and vine leaves. The reason for this is not clear. It may be due to senescence and on a par with what happens in ripening fruits—the sucrose tends to change to hexose and especially to fructose.

Maltose.—Though Brown and Morris found maltose fairly abundant in the leaves of *Tropæolum*, research conducted since on this and other plants shows this sugar as practically absent in leaves, even though these may be pronounced starch-formers.

Davis and Sawyer (1916) explain how Brown and Morris obtained comparatively high figures for maltose. The method they used for drying the material for their analyses resulted in destroying quickly the enzyme maltase which breaks down maltose to glucose leaving the less sensitive diastase (amylase to use the modern term) more or less intact to continue its hydrolysis of the leaf starch during the preparation of the material. Hence the accumulation of the maltose in the material used analytically by Brown and Morris. It looks then as if the maltose resulting from the hydrolysis of the leaf starch is immediately seized upon by the enzyme maltase and reduced to glucose, thus not permitting any accumulation of this disaccharide.

Intimate Connexion between Sucrose and Starch.—Brown and Morris in an earlier paper (1890), giving a fascinating account of the germination of some of the Gramineæ, showed that the maltose produced from the starch in the endosperm of the germinating barley seed appears as sucrose in the developing embryo, pointing to the maltose being transformed to sucrose in its passage from the endosperm into the embryo.

This exchange of starch into sucrose seems very general in plants and *vice versa*. It is distinctly puzzling and so unlike what one might have expected from their chemical structures. One is driven then to the conclusion that part of the glucose arising from the complete hydrolysis of the starch is changed at once to fructose and the two combined to form sucrose, and in the reverse direction the fructose arising from the hydrolysis of the sucrose is changed to glucose and the two glucose moieties then polymerised to starch.

Since penning these lines Prof. H. K. Porter has kindly informed me that much progress has been made recently in these directions and that a paper is to be published shortly showing how in germinating barley and wheat grains the hydrolytic products of the starch are changed to sucrose in their passage from the endosperm into the embryo and that

the necessary enzymes involved have been found in the scutellum. We await the full paper with much interest.

Though the interchange of sucrose and starch may be considered the most widespread and important carbohydrate metabolic process in plants—at any rate among the higher ones—it may be well to keep in mind the fact that there are many other reserves in seeds and vegetative storage organs which yield sugar on hydrolysis for growth. And as far as research has gone sucrose in recognizable amounts soon makes its appearance, no matter in what form the reserve may have been laid down.

On account of our familiarity with starchy seeds for our sustenance we are apt to lose sight of the fact that oily seeds are far more abundant. Thus we are presented with the problem as to how the fat is changed into sugar and particularly into sucrose during germination and early growth. Quite a recent paper bearing on this point by Konar (1958) on the developing gametophytes and embryos of *Pinus roxburghii* shows by chromatography in the 22 consecutive stages examined sucrose present in all, but glucose and fructose only in the earlier stages. He suggests the synthesis of sucrose from these hexoses.

Further it may be taken as a general rule that when storage carbohydrates of various kinds are utilised for germination of seeds or renewed growth from reserve organs, sucrose quickly makes its appearance as the circulating sugar.

Translocation.—Brown and Morris were of the opinion that the sucrose formed in photosynthesis was translocated from the leaf as hexose. Some of Parkin's results with the snowdrop leaf would appear to favour sugar travelling as hexose rather than as sucrose, but in his general discussion it is obvious that he favours sucrose rather than a hexose as the circulating sugar. Davis *et al.* (1916) from their analytical figures are strongly of the opinion that in the mangold (beet) the sucrose formed in the leaf by photosynthesis is translocated as hexose and then transformed again to sucrose for storage.

Perhaps the hexose view of translocation may be considered as more or less the prevailing one up to the beginning of the third decade of this century, when the important researches on the transport of carbohydrates in the cotton plant were published by the Trinidad investigators (*see* Mason and Maskell, 1928, and Phillis and Mason, 1933). These leave little doubt that at any rate in the cotton plant carbohydrate travels mainly as sucrose and that the sieve tubes are the conducting channels. At the same time the celerity by which this sugar can travel in these tubes is a mystery.

Formation of Starch from Sugars by Detached Leaves.—Some years ago various experiments were carried out to see how starch could be made to appear in detached leaves, previously free of this polysaccharide, when fed with solutions of various sugars and other substances akin. The plants used were largely Monocotyledons as many of these do not

form starch in their mesophyll under normal conditions. As a rule sucrose formed starch most readily.

An interesting point to whichespecial attention has been called (Parkin, 1899, p. 55) was the fact that sucrose was a better and quicker starch-former than invert sugar, *i.e.*, a mixture of glucose and fructose in equal proportions. This now suggests that either the sucrose is polymerised directly to starch without previous inversion or that the setting free of labile fructose (fructose furanose) has a quicker action on starch formation than fructose in the pyranose condition.

Excised Root Culture as Regards Carbohydrate Requirements.—This kind of culture in its general aspects has been recently excellently reviewed by Street (1957). White, one of the foremost pioneers in this form of culture, found sucrose distinctly a better source of carbohydrate than glucose or fructose or a mixture of the two. His experiments were carried out on the detached roots of the tomato plant (White, 1934). This result was challenged by Robbins and Schmidt (1938), but their experiments supporting glucose could be explained otherwise, so that, at any rate for tomato roots, sucrose is greatly preferred. It is also so for any other dicotyledonous roots which have been tested. But the preference for this sugar would appear not to apply to those monocotyledonous roots namely some of the Gramineæ—which have received this form of culture. These were found to grow equally well or even better with glucose than sucrose. It will be odd if further research allows here a distinction to be drawn between Monocotyledons and Dicotyledons.

In his Review (p. 130) Street adds the pregnant sentence—"It may also yet be possible to develop cultural conditions which permit the rapid growth of excised tomato roots on fructose and glucose".

Carbohydrate Metabolism in Animals.—It has already been pointed out that animals never contain sucrose in their tissues. It is well also to bear in mind that our knowledge of carbohydrates in animals has been largely, if not wholly, gleaned from the highest group, the Mammalia.

Though sucrose can be readily and is largely used as a food by animals, yet if it is introduced directly into the blood stream it can be recovered almost quantitatively in the urine. This shows that the internal tissues of the body have no invertive action on the sucrose, though the alimentary canal must have such action; otherwise a meal containing much sucrose should reveal this sugar in the body, which is not so.

Hence there would appear to be a marked difference between the green plant and the animal body. In the former sucrose would appear to be the chief circulating form of carbohydrate, whereas in the animal glucose with little doubt takes its place. There would appear then to be much scope for research into the carbohydrate metabolism of animals, apart from the part it is considered to play in muscular contraction.

Phosphates.—Phosphorus would now appear to be the magic element in photosynthesis and particularly in carbohydrate metabolism. Before the accelerating effect of mineral phosphates on yeast fermentation was shown by Harden and Young (1923) the role of these substances was not taken into general consideration.

Now the phosphate esters of the simpler sugars are reckoned of outstanding importance and the convenient term *phosphorylation* has been coined to embrace the interchange of these esters in carbohydrate metabolism, as concerns both photosynthesis and respiration and one might add as well muscular contraction.

It has already been pointed out that sucrose is set free in photosynthesis by removal of phosphate from a combined ester of glucose and fructose. This is most likely brought about by enzymic action. In fact at the present state of our knowledge carbohydrate metabolism would seem to centre round the interchange of these esters set going by the appropriate enzymes. Evidence strongly supports the view that phosphorylation takes place in higher plants with the production of the same phosphoric esters as are formed in yeast and muscles.

We want to be able to bring about these changes *in vitro* by the isolation of the necessary enzyme in each case. There is little doubt that the plant can change one hexose sugar into another, *e.g.*, glucose into fructose and *vice versa*. Also we want light on how sucrose can be polymerised so readily into starch and how this polysaccharide can be changed in the reverse way into sucrose.

Sugar alcohols.—The term is used here to signify those alcohols which appear associated with sugars, for example sorbitol with glucose, ribitol with ribose and mannitol with mannose. These alcohols have generally been looked upon as reduction products of monosaccharides and so, one imagines, they are not directly connected with photosynthesis.

However a recent investigation by Bidwell (1957) on two marine flagellate Algæ, *Amphidinium* and *Olisthodiscus*, is disturbing to this idea. After exposing them to photosynthetic conditions he finds no evidence of sucrose in the assimilate, but instead plenty of mannitol, whereas *Chlorella* used as a control showed sucrose in quantity. *Amphidinium* belongs to the Dinophyceæ and *Olisthodiscus* to the Heterokontæ, while *Chlorella* is a member of the Chlorophyceæ—a group of Algæ noted for producing sucrose and starch.

Haas and Hill (1929 *a*, *b*) showed some years ago that mannitol is of common occurrence in Brown Seaweeds (Phæophyceæ). Their work suggests that mannitol may be connected with photosynthesis, though they do not express themselves so. But in the summary to their first paper on sugar in these Algæ they hint that the non-reducing constituent found may possibly be a labile disaccharide and not a reserve material. One can draw the inference that if this substance be sucrose formed in photosynthesis then it is quickly transformed and utilised and so does not accumulate.

More recently Bidwell (1958) has extended his researches on the photosynthesis of marine Algæ with similar results. No sucrose was found in seven different Brown Algæ investigated—instead mannitol in quantity. Also no sucrose was found in five Red Algæ, but instead much floridoside. Whereas two Green Algæ, *Cladophora* sp. and *Ulva lactuca*, as controls showed much sucrose.

In a more detailed examination of the photosynthetic products of *Fucus vesiculosus* Bidwell *et al.* (1958) conclude that mannitol is the major soluble product.

Correlation between Mesophyll Starch and Palisade Tissue in Leaves.—The Calvin School in their survey of short-term photosynthesis in plants of 9 phyla (Norris *et al.*, *l.c.*) point out that the amount of sucrose rendered radioactive could be correlated with the extent of non-photosynthetic tissue present.

In this connexion Dr. Agnes Arber has drawn my attention to a paragraph in her book on Monocotyledons (1925, p. 75). She states that "in a very large number of Monocotyledonous leaves the whole mesophyll consists of roundish or irregular cells, and it is scarcely possible to distinguish a palisade region. The idea suggests itself that this lack of morphological differentiation may perhaps be in some way correlated with that chemical difference between the two classes, which brings many Monocotyledons into the sugar-leaved category, while Dicotyledons are prevailingly starch-leaved".

How far this correlation could be borne out by an extended investigation covering all Angiosperms, and one might add other plants as well, would make an interesting study. A basis for it was supplied years ago by Meyer (1885) who divided Angiosperms into six sections according to the amount of starch formed in the mesophyll. Monocotyledons figure largely as being often starchless. Parkin (1899) in a later investigation somewhat elaborated the starchless character of Monocotyledonous leaves.

One can imagine a well organised mesophyll with closely packed palisade cells full of chloroplasts being soon satiated with sucrose arising through photosynthesis and to prevent assimilation being stopped the sucrose is taken out of solution and stored temporarily as starch, particularly if there is hardly any adjacent non-photosynthetic tissue in which sucrose could accumulate. Or one may imagine that the means of removing the excess of sucrose quickly enough is inadequate, so starch production in the leaf is hastened. Then there is the question of the size of the cell vacuoles in which sucrose could be stored temporarily.

In this connexion it would seem that morphology and biochemistry could work hand in hand.

Discussion

Sucrose from its distribution and the use made of it as set forth in this Review would appear to be the most important sugar of green plants—

at any rate from the Green Algæ (Chlorophyceæ) upwards—in contrast to glucose for the Animal Kingdom. The query then arises was it originally the first carbohydrate to be set free when photosynthesis first began or was it evolved a little later when the Chlorophyceæ came into being? The first suggestion would seem the more likely since sucrose has been found in the generally recognised lowest group of Algæ, the Blue-green (Myxophyceæ). However much more research on the sugars of this group, as well as on other Algæ besides the Chlorophyceæ, is very desirable—particularly after the recent investigations of Bidwell and his co-workers on the Brown and Red Algæ.

That photosynthesis is carried out in a similar manner in all plants capable of it is strengthened by the fact that one pigment, chlorophyll *a*, is common to all classes of plants from the Myxophyceæ upwards. The green and purple bacteria would seem to be a little exceptional as their pigments have been found to differ slightly chemically from chlorophyll *a* and named bacterioviridin and bacteriochlorophyll respectively (Hill and Whittingham, 1956).

This brings us to the question of the origin of the Bacteria, or rather of the pigmented ones. It has been held that they are degenerate forms arising from the Blue-green Algæ. One is inclined to agree here in opposition to those who do not favour such a view. Sufficient thought does not seem to have been given to the possibility of many simple forms of life being degenerate on the analogy of yeasts being simplified ascomycetous fungi.

This brings us also to the very debatable subject as to the Origin of Life itself about which we know nothing for certain at present. It would simplify the problem considerably if we could regard life as starting with photosynthesis, but thought here has hitherto been against this simplification. Oparin (1957), the Russian scientist who has recently published a new edition of his elaborate work (fortunately now translated into English and so accessible to us all), favours a heterotrophic rather than an autotrophic origin of life as do others who have studied the question.

It is suggested that primitive organisms arose in what might be called oceanic soup and were anaerobic in character before photosynthesis became established as there was apparently no free oxygen available then.

Presumably a slow evolution of primitive forms arose heterotrophically and anaerobically and had therefore no photosynthetic ancestors. Here one might ask are there living at the present day any organisms which have never had photosynthetic ancestors? Fungi might be suggested, but I am not enamoured of such an idea. I would rather regard this group as having originally algal ancestors, though connecting links are by no means obvious.

It is axiomatic that without the green plant animal life would be quickly brought to a standstill, for it depends directly or indirectly on plants for its maintenance. But plant life as we know it—at any rate

in its higher forms—depends on bacteria, using the term in a general sense, for its supply of nitrogen in prepared forms such as nitrate or ammonium compounds, for it has been abundantly proved that such higher plants cannot make use as a rule of the free nitrogen of the air.

However it is, I presume, by no means uncertain that low forms of photosynthetic plants could originally make use of atmospheric nitrogen. Fogg (1956) in a recent review mentions many Blue-green Algæ as well as bacteria being capable at the present time of utilising such nitrogen. This then rather opens the question as to whether the green plant was not originally dependent on bacterial-formed nitrogen compounds, but was capable of using the nitrogen of the air.

It would seem on this supposition that the higher plants gave up as it were the power of using directly free nitrogen finding the bacterial-formed nitrogen compounds sufficient for their needs. But we also see these higher plants in certain cases improving their nitrogen intake by becoming symbiotic with bacteria and even with Blue-green Algæ. Legumes are conspicuous examples in this way and the alders and certain other trees and shrubs seem to be following suit.

But this digression dwelling on the nitrogen problem is taking us away from the main subject of discussion—sucrose.

It is quite clear that at various stages in the long evolution of living organisms parasitic as well as saprophytic forms have arisen from photosynthetic ancestors by losing their chlorophyll in the process. Hence as already pointed out in the Section of this Review devoted to the distribution of sucrose it would be interesting to see if this sugar ceased to be present in those forms which have discarded photosynthetic life. If so this might account for the lack of sucrose in the Animal Kingdom as a whole.

At this point one might bring in for consideration the possible interrelationships of the main groups of the Algæ. As far as fossil remains are a guide the Blue-green (Myxophyceæ) would seem to go the furthest back even to the Archaeozoic (Tiffany, 1958). They are also the most primitive from the structural point of view. Their chlorophyll is not in definite plastids but diffuse. The nucleus is ill-defined and sexual reproduction, as far as known, absent. One imagines that some form of Blue-green Algæ was the earliest of photosynthetic organisms; but their relationship to the Chlorophyceæ is by no means clear. Their carbohydrate reserve may be said not to have advanced to the starch stage but stopped at the glycogen level. Then trehalose has been reported present in some, thus pointing towards the Fungi in which this disaccharide would appear to be general. They may to some extent be degenerate, but yet one must bear in mind their cosmopolitan character, both as regards distribution and habitat, and then they may be said to support Willis's Age and Area Theory.

The Chlorophyceæ date back nearly as far, namely to the Ordovician, the Rhodophyceæ equally so, the Phæophyceæ only to the Silurian and

the Xanthophyceæ somewhat later to the Devonian. The Diatoms apparently do not appear until the Triassic.

Here one may venture on some speculations. Granted that the Chlorophyceæ arose in water originally fresh, then one can imagine from such a medium some forms stepping on to the land gave rise to the higher plants. On the other hand, others managed to adjust themselves to salter seas and evolved into such large groups as the Browns and Reds which at the present day are largely marine with no obvious relationship to the higher plants.

At this point though this Review has already considered resemblances between the Red and Blue-green Algæ as parallelisms I am rather inclined to hold on second thoughts that the former came directly from the latter without the Chlorophyceæ intervening as it were. Besides the additional pigments they have in common, both groups are non-flagellate and even trehalose has been declared present in one genus of Red Algæ.

On the above supposition one may hazard the guess that the carbohydrate metabolism underwent a change and that the sucrose set free in photosynthesis ceased to accumulate, but was quickly changed into other forms such as mannitol in the Brown and floridoside in the Red Algæ in accordance with the recent Bidwell investigations. In this connexion it might be of interest to see if the carbohydrate metabolism of the Angiosperms which have taken to a complete marine life, such as *Zostera* and its ally *Phyllospadix*, differs markedly from that of Angiosperms generally.

Then again it is possible that in some Angiosperms another form of circulating (widely distributed) carbon compound such as a sugar alcohol has taken the place of sucrose. On looking back at Meyer's paper (1886) on feeding (destarched) leaves on sugars and sugar alcohols, though sucrose as a rule proved the best starch-producer, his results give some marked exceptions, for instance the Oleaceæ. As a family it would seem to form starch in the leaf more readily from mannite (mannitol) than from sucrose. A plant of this character might therefore be well worth investigating under modern technique to see if such a sugar alcohol takes the place of sucrose as a circulating carbohydrate.

Now let us come finally to the discussion of the metabolism of sucrose in the Angiosperms, as it is here where most of the work and thought have been concerned with the interrelationship of sucrose and starch—a subject which at the present time is being vigorously investigated by Professor Helen Porter and her associates at the Royal College of Science.

Though the interchange of sucrose and starch is perhaps the most widely spread phenomenon of carbohydrate metabolism, one must not lose sight of the fact that in the higher plants other polysaccharides are often stored in place of starch or alongside of it and further oil, especially in seeds, may take the place of carbohydrate. All these storage products

would appear when wanted for growth to be hydrolysed down to sugar and mainly to sucrose. Here then is a large field of research to trace step by step how these changes are brought about and one might add how in the reverse direction these storage products are laid down from the simple sugars.

From modern research two major principles would seem to be involved, namely, enzymic action and phosphatic esterification of the sugars.

Not so many years ago the chemical constitution of an enzyme was a mystery. Now we know that they are mainly protein in character, and the thought suggests itself that the distinction to be drawn between true proteins and enzymes may be a fine one. There seems to be no end of enzymes and one hazards the idea that a protein—perhaps simplified in molecular structure—may if the need arises become enzymic, particularly by adding to itself what is known as a prosthetic group. One might by way of illustration and as a rough analogy compare this idea with catalysts of inorganic chemistry, for instance the element platinum can act as a catalyst under certain conditions, yet ordinarily it behaves as a metal giving salts, etc.

Now that some enzymes can be isolated in the crystalline state it is not difficult to imagine that at a not too distant date carbohydrate transformations may be readily brought about *in vitro* by bringing together the appropriate enzymes to act, say, on phosphatic esters of sugars. To be able to change at will *in vitro* maltose into sucrose and fructose into glucose would seem to be desirable targets.

Then we badly want to know the value of Y fructose in plant metabolism. Onslow (1931) considered it to be probably the substrate for respiration. Perhaps this can hardly be maintained at the present time. But at any rate the importance or otherwise of fructofuranose as one of the two components of sucrose is by no means settled, and until we know more we can hardly answer the question why this disaccharide should have been selected for the green plant rather than one giving glucose solely on hydrolysis like say, maltose.

Though *free* fructose as far as we know is never to be found either *in vitro* or *in vivo* in the furanose state, since as soon as it is set free from sucrose it changes at once into the pyranose condition, yet it does exist in the Y form in combination with phosphate as esters and is even found so in muscles.

It is tempting to assign different functions to the two components of the sucrose molecule, but none of the suggestions so far put forward has been proved actually to happen. Rather the two hexoses derived from the inversion of the sucrose form a kind of common pool and from this sugar is drawn for various needs. Regarding starch formation Porter and May (1955) in their experiments with tobacco leaf discs conclude that fructose and glucose free or combined in sucrose are equally available for starch synthesis and that there can be no question of the preferential utilisation of one or other hexose.

That fructose and glucose are interconvertible in the green plant can hardly be doubted, but how this is brought about is still largely an unsolved problem. Most likely phosphorylation and enzymic action are mainly involved.

Then it is difficult to believe that the constitution of sucrose is not of prime importance in the metabolism of the green plant taking into consideration the fact that when the fructose is set free by inversion it is in the labile reactive furanose state. Thus the sucrose molecule differs from other disaccharides such as maltose which is wholly composed of pyranose-glucose components.

It is therefore somewhat surprising that the plant has not managed to evolve for storage purposes a saccharide of a higher degree which on hydrolysis would yield sucrose direct without having to take the roundabout way of obtaining its sucrose from starch. The only attempts that way would seem to be the trisaccharides gentianose and raffinose from which by appropriate enzymes sucrose can be liberated leaving behind respectively glucose and galactose.

Summary

1. The disaccharide sucrose would appear to be peculiar to the *green* plant and seems to be the first sugar to be set free in photosynthesis. But further research on the marine algæ is needed to substantiate this claim.

2. From the Green Algæ (Chlorophyceæ) upwards it would appear to be the chief circulating sugar. When in excess it is condensed to starch as a rule.

3. The interconversion of sucrose and starch is of general occurrence and of paramount importance.

4. No matter in what form carbohydrate may be stored, on hydrolysis sucrose soon makes its appearance.

5. The greater preponderance of sugar, especially sucrose in leaves of the Monocotyledons, may be correlated with the lack of palisade tissue in them as compared with the dicotyledons.

6. The interchangeability of carbohydrates is largely brought about by the formation of phosphatic esters coupled with enzymic action.

7. During active photosynthesis the evidence points to great fluctuation in the percentage of sucrose during a day of 24 hours with little change in that of hexose sugar.

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ROOT APICAL MERISTEMS IN MONOCOTS

I. Root Apex Organisation in Some Members of the Amaryllidaceæ*

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(Received for publication on February 15, 1959)

Introduction

The earliest classifications of root apices by various authors like Janczewski, Treub, Flahault and others have been reviewed by Popham (1952). Schade and Guttenberg (1951) described root apex organisation in a few members of the monocotyledons. Clowes (1954, 1956) published an account of promeristem and nucleic acids in the root apex of *Zea*.

Materials and Methods

Material for this study was collected during botanical excursions of Birla College, Pilani. The material was fixed on the spot in different fixatives and then transferred to 70% alcohol.

The following species were taken for the investigation:—

1. *Haemanthus coccineus* L.
2. *Zephyranthes tubispatha* Herb.
3. *Eucharis grandiflora* Planche. Linden.
4. *Amaryllis belladona* L.
5. *Crinum latifolium* L.
6. *Agapanthus africanus* (L.) Hoff.

Agapanthus africanus was sent to the author by Dr. Hecht of State College of Washington. The author is thankful to Dr. Hecht for the same.

Usual procedures of dehydration and embedding were followed. In addition to the safranin-fast green combination, methyl green and pyronin were also used. A few preparations were stained with toluidine blue. The two latter combinations proved better for revealing the colour zonation in the apex.

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* A part of the work approved for Ph.D. award of Rajasthan University.

Observations

Haemanthus coccineus

The median longitudinal section shows two plates of cells at the apex (Text-Fig. 1). The lower tier of initials has two prominent isodiametric cells forming dermo-periblem complex. From these cells on the lower side start the rows of columella. The second tier of initials has two cells forming stelar initials. The sides of the cap are formed by the distinct calyptrogen occurring just beneath the dermatogen. Columella appears to be independent of the sides of the cap.

Zephyranthes tubispatha

The root apex shows three sets of superimposed tiers of cells. The lowermost set has three centrally placed cells on which abut the first cells of dermatogen (Text-Fig. 2). Next two tiers of three cells each form initials of periblem and stele. There is a distinct calyptrogen.

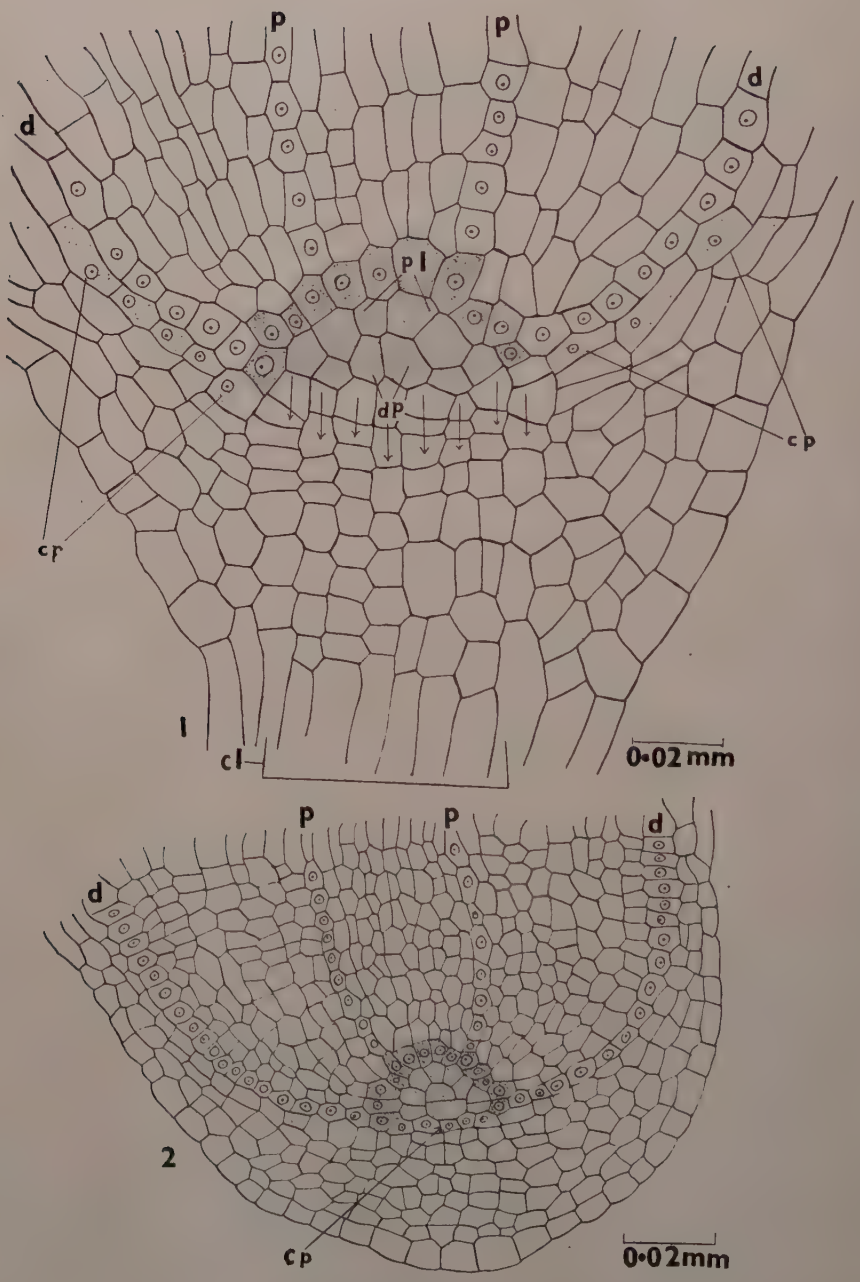
The apical organisation of *Eucharis grandiflora* and *Amaryllis belladona* resemble each other and is different from the earlier types (Text-Fig. 3). Here the apex does not show any arrangement of cells in tiers. All the rows of tissue appear to start from a group of prominent cells at the apex (stippled cells containing nuclei, Text-Fig. 3).

Crinum latifolium and *Agapanthus africanus* resemble each other in the organisation of root apex. The photomicrograph shows a broad columella, the middle rows of which appear to touch the stelar initials. On both sides of the columella rows there occurs a row of prominent cells arranged in a superimposed fashion and spreading towards the apex. These cells give rise to complete root body. Sides of the cap appear to proliferate from the dermatogen.

All these apices, when stained with methyl green-pyronin combination, show a region at the apex (lightly stippled cells in which nuclei are not, shown) where the cytoplasm is less densely coloured red than the surrounding cells (densely stippled cells with nuclei, Text-Figs. 1, 2, 3). The less densely coloured zone which is the 'quiescent centre' includes the plates of the stele and the dermo-periblem complex and a few cells occurring near these plates of initials. There is a gradual increase in the density of colour from this region to the surrounding cells, but there is a sharp boundary between the first row of cap cells and adjacent cells of the less densely stained zone, the 'quiescent centre'.

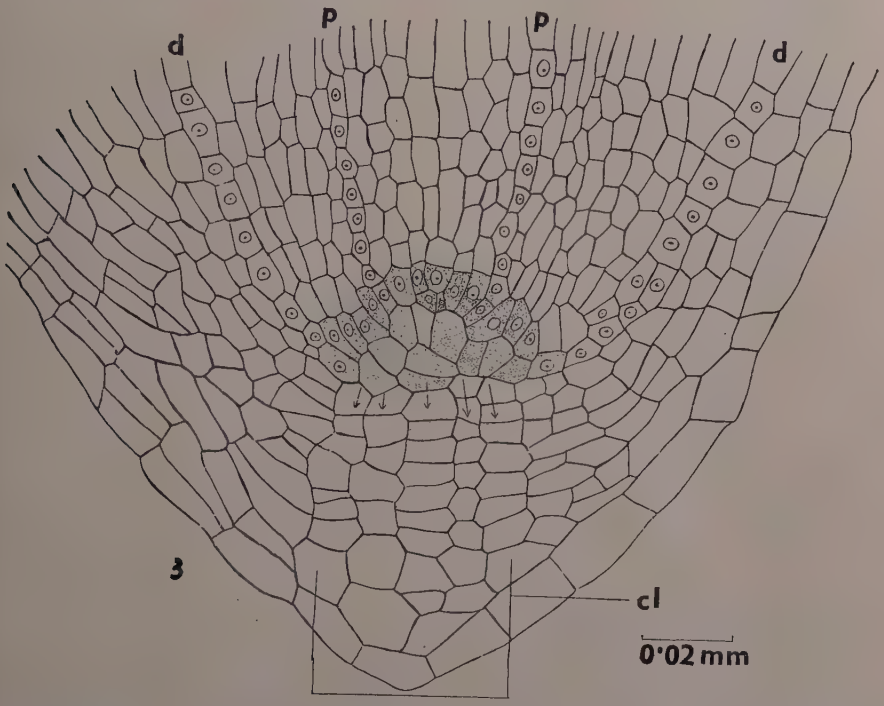
Discussion

The apical construction described for the species investigated falls under the following categories. The first type where there are three distinct tiers of cells at the apex is observed in *Zephyranthes tubispatha*, the second where there occur only two tiers is found in *Haemanthus coccineus* and is reported to occur in grasses also. These correspond to the third and second types respectively, as mentioned by Esau (1953).



TEXT-FIGS. 1–2.

TEXT-FIGS. 1-2. Fig. 1. Median longitudinal section of the root apex of *Haemanthus coccineus*. Lightly stippled cells shown without nuclei is the quiescent centre. Densely stippled cells with nuclei occurring on the surface of the quiescent centre are the proper root initials. *d*=dermatogen, *p*=pericycle, *dp*=dermo-periblem complex, *cl*=columella, *cp*=calyptrogen, *pl*=plerome. Fig. 2. Same of *Zephyranthes tubispatha*. *d*=dermatogen, *p*=pericycle, *cp*=calyptrogen.



TEXT-FIG. 3. Median longitudinal section of the root apex of *Eucharis grandiflora*. *d*=dermatogen, *p*=pericycle, *cl*=columella.

The next type, where the cap, dermatogen and the cortex have common groups of initials and the stelar pole independent, is observed in *Agapanthus* and *Crinum*. Such a type of organisation is quite common in monocotyledons and has been described earlier by Treub* (1876) and Flahault* (1878) for many members of different families of monocotyledons including a few members of the Amaryllidaceæ. The type observed in *Eucharis* and *Amaryllis* has common initial zone for all the tissues and it corresponds to the fourth type given by Esau (1953) but the figure [*Allium sativum* (Mann, 1952), mentioned by Esau, 1953, pp. 117] resembles more to the earlier type found in *Crinum* and *Agapanthus*.

* Reviewed by Popham (1952).

In the light of the present observations it will be worthwhile attempting to interpret root apical meristems in terms of a few important existing theories.

As far as the histogen concept is concerned it is applicable only to *Zephyranthes* in which the arrangement of cells at the summit of the apex occurs in superimposed tiers. But here predestination of tissues, which is one of the requisites of histogen theory, should be put aside.

The idea of an 'inverted cup' promeristem of Clowes (1953) is worth consideration. The so-called tiers or the group of initials in the investigated apices have surrounding them cells staining deeply than the cells at the summit which sometimes appear vacuolated. The shape of these cells, when considered *in toto*, appears like an 'inverted cup' the bottom of which is formed by the stelar initials and the sides by the derivatives of dermo-periblem complex. Clowes (1954) clearly differentiates between the minimal constructional centre and the cyto-generative centre. According to him the 'initial group' of Burmfield (1943) and 'central cell' of Schade and Guttenberg (1951) are the minimal constructional centre. Thus the so-called initials which keep the pattern of root apex are the cells of the minimal constructional centre.

The 'cup-shaped' promeristem hypothesis implies the assumption that all the cells at the apex are meristematic. But as seen in the present study the cells at the pole of the stele and the cortex are not observed in the state of division. So the cup-shaped idea would not serve the purpose of interpreting these root apices.

The most suitable way to explain these root apices would be on the basis of the 'quiescent centre' hypothesis put forward by Clowes (1956). The shape of the quiescent centre (cells shown without nuclei and stippled lightly in the figures) is roughly like the frustum of sphere. The base of the quiescent centre lies apposed to the cells of the first layer of the root cap. It includes the poles of the stele and the cortex-epidermis histogens. The cells of the quiescent centre have rarely been observed to divide. The quiescent centre is surrounded by the cells (cells with nuclei stippled densely in the figures) which appear in an active state of division and which form the true root initials. From these cells further development of tissues takes place.

The quiescent centre is probably equivalent to the 'central mother cells' zone met with in certain shoot apices. Lance (1952) states that the mitoses in the central region of the shoot apex of *Vicia faba* were almost absent while they were very frequent in the surrounding region to which she attributes the origin of all the tissues. Somewhat similar situation is observed in these root apices, though the cells of the central region in case of shoots remain quiescent only during vegetative phase. The so-called apical initials in these roots may have organised the apex during embryonic stages or while the embryo is germinating, but thereafter the apical initial region remains quiescent.

The rows of the columella in the cap of *Agapanthus* and *Crinum* run up into the cortex and stele. This fact has led some workers to hold that the promeristem could be reduced to a single cell functioning as an apical cell (Guttenberg, 1947). Others think that there occurs a transverse meristem which gives rise to both cap cells on the lower side and stele and cortex cells on the upper side. According to the present observations both these views are unlikely. In the first instance, as already pointed out, promeristem in these roots consists of all the cells occurring on the surface of the quiescent centre, the boundary of which fluctuates towards the root body side as has been revealed by the gradual transition in the density of red colour when stained by methyl green-pyronin combination. Secondly there would not be a quiescent centre at all if the initial plates or the transverse meristem added to the cells of the stele and the cortex, unless the immediate derivatives stopped dividing for a while and resumed their activity after they had been displaced to a position several cells away from the transverse meristem. If this occurred it would be rather difficult to account for the continued divisions on the surface of the quiescent centre and also for the sharpness of the boundary between the quiescent centre and the cap cells.

The quiescent centre hypothesis is based upon the synthesis of nucleic acids as has been revealed by differential density of stain in this region. The cells surrounding the quiescent centre show denser staining indicating the synthesis of DNA which implies the cell division while the cells of the quiescent centre take a very light stain indicating their quiescence.

Summary

In the present paper three theories, *viz.*, histogen theory, inverted cup concept and the quiescent centre concept have been discussed to explain the root apical meristem of the members investigated. Careful comparison would reveal that the most suitable concept is the "quiescent centre" which is based upon the synthesis of nucleic acids.

Acknowledgement

I express my sincere gratitude to Dr. B. N. Mulay for his valuable guidance and keen interest in the work. I am also thankful to Dr. F. A. L. Clowes of Oxford University for his valuable suggestions. My thanks are also due to the Ministry of Education, Government of India, for the grant of a research fellowship during the tenure of which this work was undertaken.

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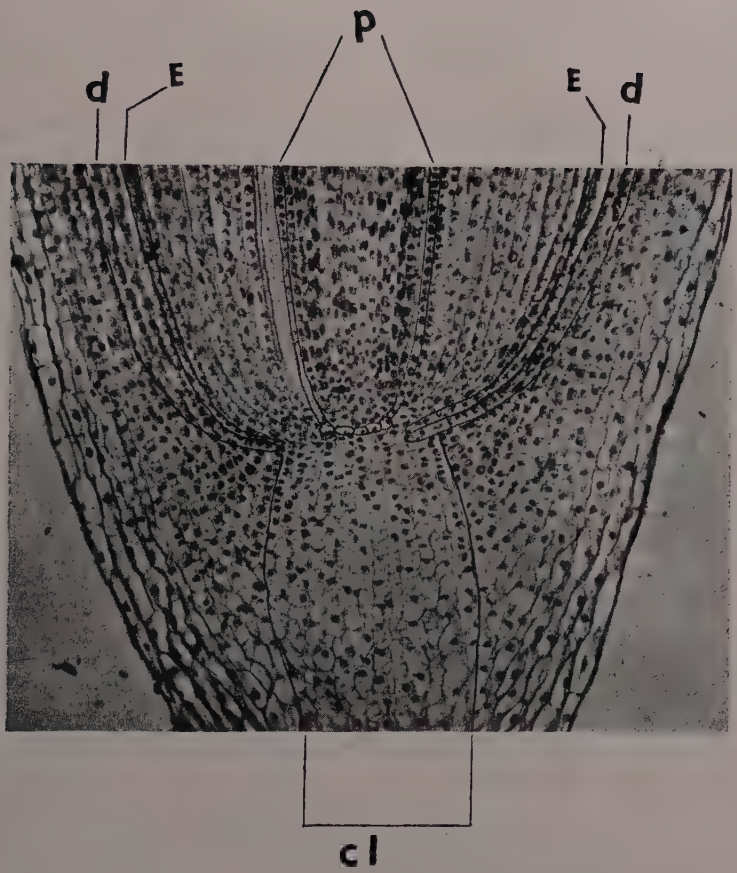
EXPLANATION OF PLATE III

Photomicrograph showing the median longitudinal section of the root apex of *Agapanthus africanus*. A few layers are retouched for the sake of clarity. *d*=dermatogen which becomes many layered behind the apical region; *e*=exodermis, *p*=pericycle. Four cells at the apex on which abut the first cells of the pericycle are the stelar initials.



B. D. Deshpande

SOME OBSERVATIONS ON THE GAMETOPHYTE OF *HYPODEMATIUM CRENATUM* (FORSK.) KUHN WITH A NOTE ON THE PHYLETIC AFFINITIES OF THE GENUS

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The genus *Hypodematium* Kunze has somewhat doubtful phyletic affinities and as indicated in an earlier communication (Mehra and Loyal, 1956), various authors have associated it with quite different genera in their systems of classification. The morphology of the sporophyte and the chromosome number were reported earlier (Mehra and Loyal, *loc. cit.*). The present paper aims to record the development and structure of the gametophyte. The affinities of the genus are discussed in the light of characters of its sporophytic and gametophytic generation.

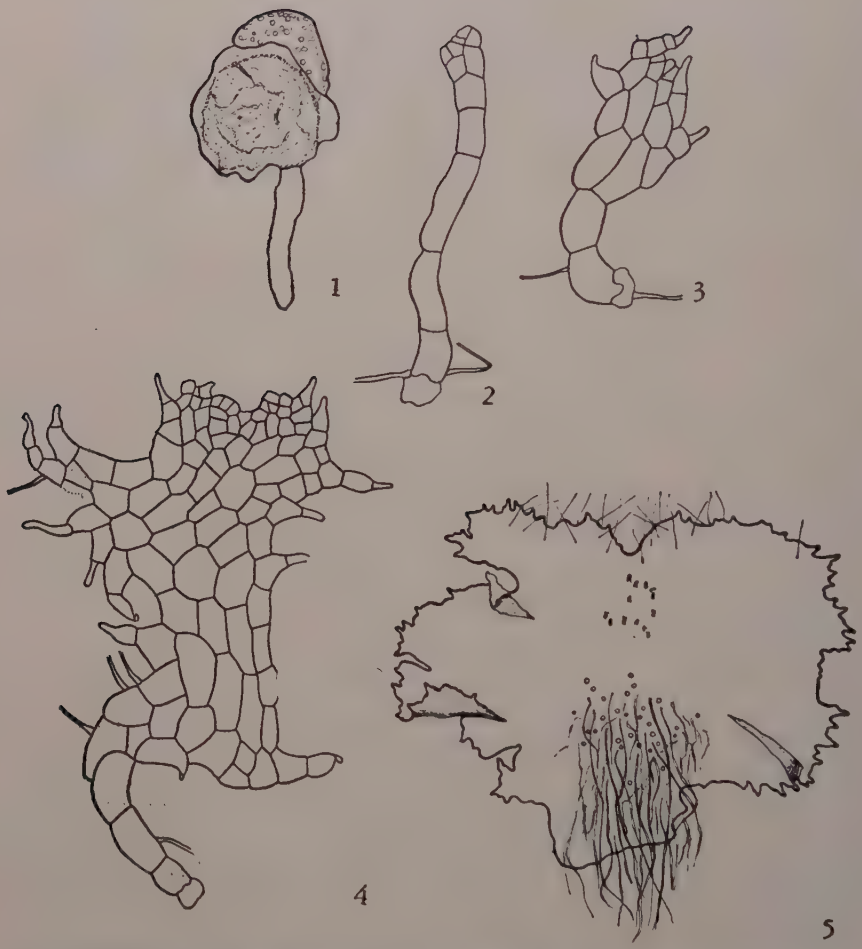
Material and Method

Ripe spores were collected from Mussoorie in September 1956. Cultures were raised on Knop's solution, as well as on sterilized canal soil in Petri-dishes. Observations are based on fresh material [for clarification of fresh material Davie's (1951) method was used] but for sex organs sections were cut of the prothalli embedded in paraffin after fixation in half strength acetic-formaline (*cf.* Manton, 1950). Thickness of sections was kept at 10 μ and the stain used was safranin and fast green in combination.

Observations

The spores are monolete, dark chocolate brown, with a perispore. The structure in general resembles that of *Dryopteris* and *Tectaria.** Germination occurred on Knop's solution in 5–6 days and was much earlier than on soil. The exine ruptures separating the two flat sides of the spore and a papilla soon emerges, from which at its basal region a rhizoid develops (Text-Fig. 1). The papilla gives rise to a filament of 2–5 cells. Broadening of the filament is brought about by the activity of a two-sided apical cell which cuts off segments right and left in the usual fashion (Text-Fig. 2). Some of the marginal cells of the plate

* Kachroo (1956, pp. 103) reports tetrahedral spores in two species of *Tectaria*. Observations by the writer on several Himalayan species of *Dryopteris* and *Tectaria* reveal that tetrahedral spores are absent in these genera.



TEXT-FIGS. 1-5. Development of the gametophyte. Fig. 1. First prothallial cell and rhizoid, ×175. Fig. 2. Young plate stage with an apical cell, ×90. Fig. 3. Fifteen days old prothallus, filamentous projections and marginal glands are noticeable, ×90. Fig. 4. One month old prothallus, ×90. Fig. 5. A fully developed cordate prothallus, 4 months old, note the bristles around the notch, ×10.

undergo division forming 2–3-celled tooth-like projections, the terminal cells bearing capitate glands (Text-Figs. 3–4). The appearance of these marginal glands at such an early stage is a constant feature of the species and is also shared by several species of *Dryopteris* and *Tectaria* studied by the writer.

At this stage the prothalli on Knop's solution were transferred to sterilized canal soil. Within a period of $1\frac{1}{2}$ months an almost symmetrical cordate prothallus is formed (Text-Fig. 5). The margin of

the prothallus is highly uneven because of the pronounced development of marginal filaments each ending in a capitate gland. Besides the presence of these glands on the margin as well on both the surfaces, some fully developed gametophytes produce long bristles especially near the notch region (Text-Fig. 5). These are similar to those on the lamina of fronds. Four months old prothalli generally show degeneration of the filamentous portion and there is a profuse growth of rhizoids on the ventral surface.

Antheridia appear on $1\frac{1}{2}$ months old cordate prothalli but on filamentous ameristic prothalli they may appear much earlier. As characteristic of most of the ferns, the larger prothalli form mostly archegonia and only a few antheridia. The smaller irregular plates or ameristic prothalli produce only antheridia in abundance.

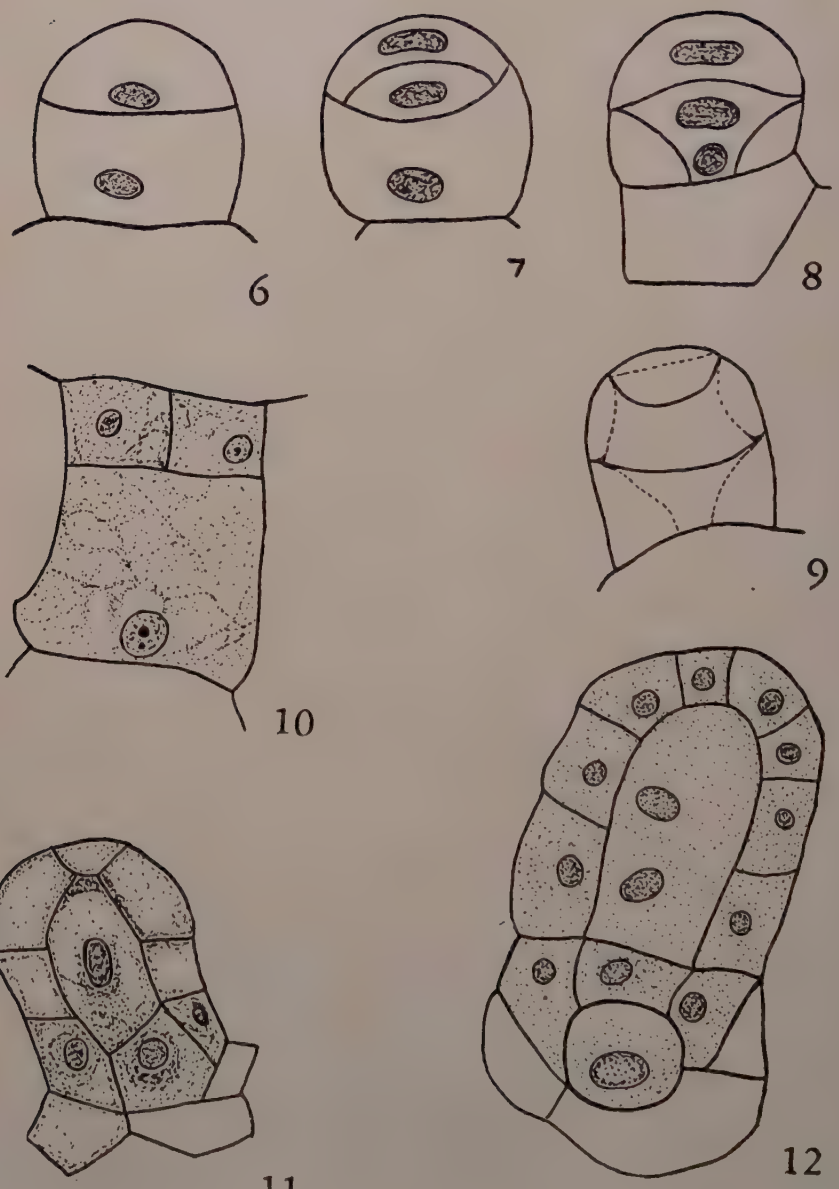
The development and structure of the antheridium are as usual for advanced leptosporangiate ferns. The mature antheridium is globular or slightly elongated. Generally they are sessile but rarely there may be a well-developed stalk. The antheridium initial arises as a protuberance from a superficial cell which divides by a transverse wall into a large basal cell and an upper smaller cell (Text-Fig. 6). The basal cell remains undivided. The upper cell divides into an outer wall cell and an inner dome-shaped cell in the usual fashion (Text-Fig. 7). Next, the wall cell segments an opercular cell which remains undivided (Text-Figs. 8–9). The inner cell forms the spermatogenous tissue.

The archegonium develops in the customary way from one of the superficial cells on the ventral side. It divides by a transverse wall into an outer primary neck cell and a larger inner cell (Text-Fig. 10). The former divides by two vertical intersecting walls into four neck initials which form a neck of four rows of cells. The neck of mature archegonium is almost straight and consists of 4–5 cells in a row. The inner cell divides transversely into a ventral cell and a neck canal cell (Text-Fig. 11). The neck canal cell becomes binucleate. The ventral cell divides into a small ventral canal cell and a large egg (Text-Fig. 12).

Discussion

Ching (1935 *a*) suggested that the genus *Hypodematium* is neither related to *Dryopteris* nor to *Thelypteris*; later on (1938) he revised his opinion and included it in Thelypteridaceæ, considering it a close relative of the genus *Lastreopsis*. Copeland (1947) maintained the original view of Kunze and indicated its affinity with *Woodsia*. Recently Holttum (1954) expressed his agreement with Ching (1938) but favoured the inclusion of both these genera (*Lastreopsis* and *Hypodematium*) in the subfamily Tectarioideæ (*sensu* Holttum). Before any suggestion is made with regard to the relationships and proper systematic position of the genus, a survey of all the available characters of the genus is necessary.

All the three species of the genus described by Ching are characterized by dorsiventral creeping rhizome with a corresponding stelar system



TEXT-FIGS. 6–12. Figs. 6–8. Development of antheridium. Fig. 9. Mature antheridium. Figs. 10–11. Archegonium, stages in development. Fig. 12. Mature archegonium as observed on the clarified gametophyte. All, ×760.

(Ching, 1935 *b*; Mehra and Loyal, *loc. cit.*). This character, to the writer's knowledge has not been recorded so far in any of the genera of Dryopteroid, Thelypteroid and Athyroid ferns. Dorsiventral character of the rhizome is perhaps correlated with the habitat of a species, which is evidenced by the fact that generally (although not invariably) it is observed in the rock dwellers and epiphytes of several members of the families Grammitidiaceæ, Aspleniaceæ, Polypodiaceæ (*sensu-stricto*) and Elaphoglossaceæ. Furthermore, the inconsistent nature of this character within the boundary of a single genus is well exemplified by *Elaphoglossum* (Bell, 1950). In the various species of this genus the posture of the rhizome and stelar system varies with the habitat. Thus it is reasonable to regard this state of the rhizome as derived one (*cf.* Bower, 1923; Dickason, 1946) and in the present situation cannot be considered as a dependable criterion for comparison.

In having a binary leaf-trace, and in the structure of individual vascular bundle, on broad pattern, this genus resembles *Thelypteris*, *Cyclosorus*, *Athyrium* (including *Diplazium*, *cf.* Copeland, *loc. cit.*; Holttum, 1949) and *Cystopteris*. In contrast to this, Dryopteroid and Tectarioid ferns possess a highly complex leaf-trace comprised of two large adaxial bundles and a variable number of smaller strands constituting the abaxial arch. Evidently, the stipe anatomy is strongly suggestive of its relationship with *Thelypteris* and *Athyrium*. But the unicellular needle-like hairs on the scales of *Thelypteris* are completely lacking in the present genus. Here the scale margin is often glandular and possesses marginal filaments.

In general frond form, the genus agrees well with *Lastreopsis* and decompound leaved species of *Dryopteris*, *viz.*, *D. sparsa*. It is probably on this ground that Ching (1938) and Holttum (1954) related *Hypodematium* with *Lastreopsis* which unlike the present genus possess 'Ctenitoid' hairs. It may be added that superficial resemblance cannot be given much importance as a source of comparative evidence since it is not uncommon to find similar cases of resemblance of leaf-architecture in several unrelated members of the filicales. The presence in *Hypodematium* of long needle-like hairs on the rachis, lamina and indusium is a Thelypteroid character and is also shared by some species of *Athyrium*. In a Chinese species, *viz.*, *H. cystopteroides* the hairs are short, glandular, much like those of *Cystopteris tenuisecta*.

The gross soral character and its position in *Hypodematium* resembles with *Dryopteris*, *Thelypteris* and some primitive species of *Athyrium*. The indusium in *H. crenatum* shows remarkable resemblance with some species of *Athyrium*, while its attachment is 'Cystopteroid' in *H. cystopteroides* (Ching, 1935 *b*).

As stated earlier the gametophyte of *H. crenatum* resembles that of several species of *Dryopteris* and *Tectaria* in having a highly unequal margin of the prothallus and the origin of glandular hairs at a very early stage of its development. On the other hand, in the principal genera of Thelypteridaceæ (unpublished data by the writer) the

prothallus lacks marginal projections, and glandular hairs appear rather late and sparingly.

From a purely cytological consideration its relation with Thelypteroid ferns seems improbable because these genera have 36 chromosomes as the monoploid number (lesser numbers also in some species of *Thelypteris*), while the present species and the genera of Dryopteroid affinity including *Woodsia*, *Tectaria*, *Athyrium* and *Cystopteris* are all based on 40, 41 and 42.

Thus, it is seen that *Hypodematium* represents a peculiar combination of characters of such genera as *Woodsia*, *Dryopteris* and *Lastreopsis* on the one hand and *Thelypteris*, *Athyrium* and *Cystopteris* on the other. In some major characters like grooved pinnæ and pinnules, stipe anatomy, scales, soral structure, indusium and chromosome number, it has greater resemblance with *Woodsia*, *Athyrium* and *Cystopteris*. It is fairly certain that *Hypodematium* represents a group of specialized genera (others being *Athyrium* and *Cystopteris*) all of which have probably evolved more or less independently from an early *Dryopteroid* stock. In the present situation, it seems reasonable to associate the present genus with Athyriaceæ (*sensu* Alston, 1956).

Summary

The gametophyte of *Hypodematium crenatum* is described. It is shown that the gametophyte resembles those of *Dryopteris* and *Tectaria* in having a highly uneven margin owing to the presence of filamentous projections and the appearance of capitate glands at a very early stage of its development. The evidence from the available data of morphology of the gametophyte as well as sporophyte and chromosome number strongly suggests the early Dryopteroid ferns as the primogenitors of the present genus. But it appears to have followed a distinct line of evolution close to *Athyrium* and its relatives. Its inclusion in the family Athyriaceæ (*sensu* Alston) seems to be a satisfactory solution.

Acknowledgement

The writer is deeply indebted to Prof. P. N. Mehra for his valuable guidance and helpful comments during the course of present study.

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A CONTRIBUTION TO THE EMBRYOLOGY OF *BEGONIA CRENATA*

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(Received for publication on March 2, 1959)

Embryological information on the Begoniaceæ has been rather inadequate. Schnarf's (1931) survey indicates that what little literature is available is too scattered and casual. The summary given by him is the only cumulative information to this day. The most important, and at the same time, detailed investigation is that of Sandt (1921), who demonstrated amongst other things, that the endosperm is free nuclear and that at maturity the embryo is surrounded by a single persisting layer of endosperm cells, whose histological features simulate the cells of the embryo.

The species under investigation was collected in the forests of Poringalkuthu (Chalakudi), Kerala State, during September 1958. The herbarium specimens bearing field number E.G.R. and B.G.L.S. **2985** have been deposited in the *Herbarium Collegii Presidentiæ Madrasensis.* In the natural habitat, the plant is a slender herb not more than 6″ tall, growing on wet rocks and boulders in the neighbourhood of water courses under dense forest cover. Careful analysis of the plant parts indicates that the Poringalkuthu plants are most nearly allied to *Begonia crenata* Dryand., as could be determined by taxonomic descriptions. Our plants do not possess a tuberous rhizome or root-stock, as stated to be one of the features of the typical *Begonia crenata* by Hooker (1879) and Gamble (1919). If the root-stock nature is a variable character depending upon whether the plant is epiphytic or terrestrial, then the Poringalkuthu plants may be taken to represent one of the variables. On the other hand, if the presence of a root-stock is a consistent feature for *Begonia crenata*, the taxonomic status of the Poringalkuthu plants deserve to be studied more carefully by taxonomists. The second point in which the Poringalkuthu plants differ from the taxonomic descriptions concerns the shape of the leaf, in that it is *not* cordate and in that the longitudinal halves of the leaf, again, are *not* unequal in size or shape, in contrast to the descriptions given by Hooker (1879) and Gamble (1919) respectively. Thirdly, Gamble notes that the two sepals in the staminate flower are orbicular; in the Poringalkuthu specimens they are distinctly and consistently ovate or elliptical. In this connection, it may incidentally be mentioned that in the *Herbarium Collegii Presidentiæ Madrasensis* are two specimens of *Begonia*, one collected at Jog bearing field number **6613** of *P.F. Fyson* and the

second one secured from Alevur, South Kanara, on which the herbarium voucher is incompletely filled. Both these specimens have been determined by P. F. Fyson as *Begonia crenata* Dryand. A re-examination of these sheets indicates similarities of morphological features to the Poringalkuthu specimens, even to the extent of the differences noted above. Thus, while we are certain that the plants used in the present investigation are conspecific with the herbarium specimens mentioned above, we are yet unable to conclude the exact taxonomic identity of these plants. Therefore, it should be emphasized that the specific epithet for the Poringalkuthu plants has been used with reservation.

The earliest stage in the development of anther available to us shows from the outside, epidermis followed by two- or of irregularly three-layered parietal tissue and an innermost layer of tapetum. The cells of the last layer are binucleate and their function conforms to the secretory type. The microspore mother cells divide meiotically in simultaneous manner and the individual microspores are separated by the process of furrowing. At maturity, the cells of the anther epidermis become conspicuously protuberant and sometimes even slightly papillose. The walls of the subepidermal layer exhibits thickenings characteristic of endothecium. As observed by Elfving (1879) in other species of the genus, the pollen grains are shed at the two-celled condition.

As in the species investigated by Sandt (*B. tuberosa*, *B. Frœbeli*, *B. hirtella*, *B. manicata*, *B.* "*Knollenbegonien*"; 1921), the ovule of *Begonia crenata* possesses tenuinucellus with two integuments. Both inner and outer integuments are two-layered until the time of fertilization. During post-fertilization development, the number of cell layers constituting the outer integument may increase to 3 or 4 layers due to the divisions of the inner layer of cells. The volume of nucellus is very small, being limited to an axial row of three to five cells, this group being enveloped by an epidermal layer. With the differentiation and growth of the megaspore mother cell, the nucellus becomes disorganized excepting for a few parietal cells at the micropylar end. Thus, very soon, the embryo-sac comes to lie in contact with the cells of the inner layer of the inner integument. During pre-fertilization stages, the cells of this layer of the integument assume a more or less cubical contour and the layer as a whole becomes morphologically distinct from the other cell layers of the integument. We contend that this layer is homologous to the so-called "integumentary tapetum", a common feature in many sympetalous families. However, it must be emphasized that its expression in *B. crenata* does not attain as conspicuous a degree as in the latter families. In connection with the development of the embryo-sac Sandt (1921) observes: "Bis auf eine Lage palisadenartiger Zellen, die eine Epithelschicht um den Embryosack und seine Verlängerung nach der Chalaza hin bilden, werden die inneren Zellagen des Nucellus vom Embryosack bei seinem Wachstum bis zur Reife verdrängt." This statement appears to us to have left the origin of the "epithelium" ambiguous. Sandt's statement appears to imply that it is the outermost layer of the nucellus that differentiates into the

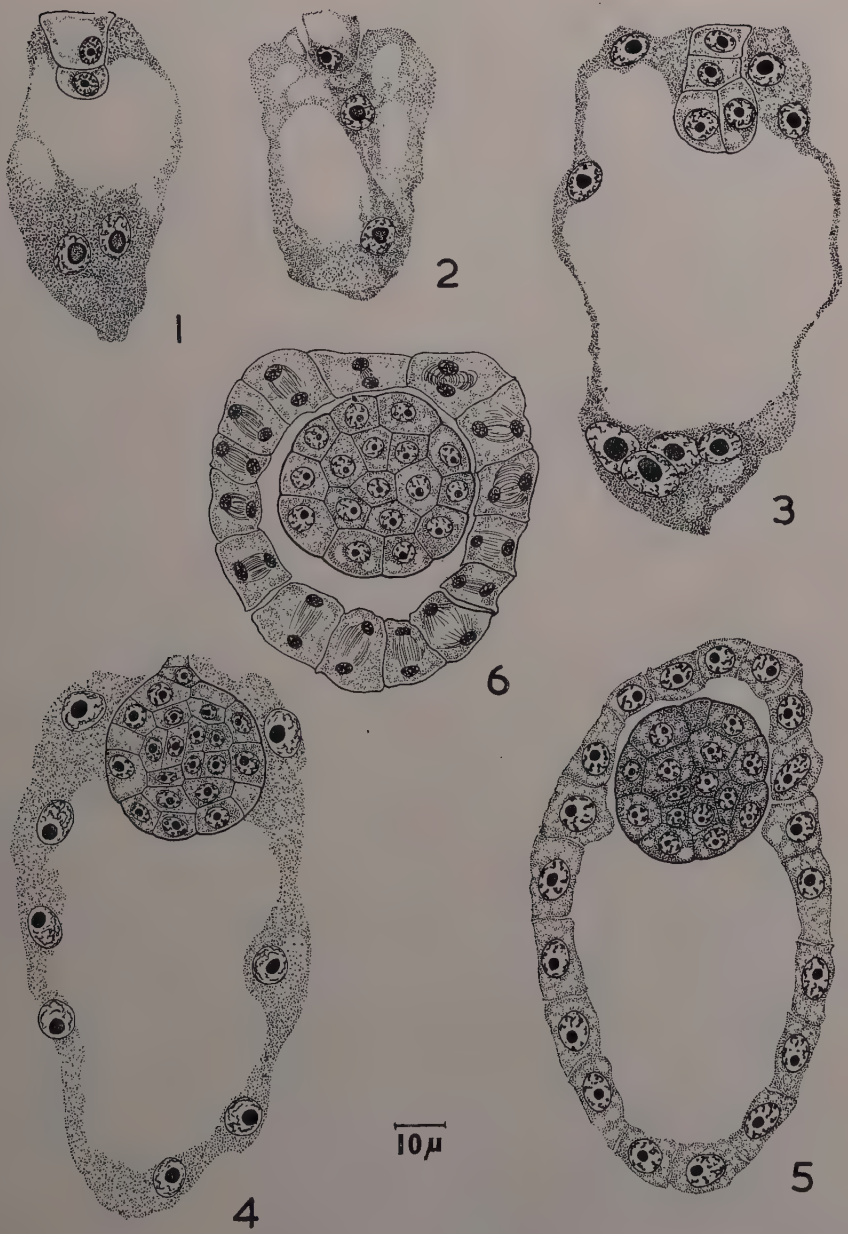
"epithelium". As has been pointed out earlier, the megaspore mother cell or the embryo-sac which undergoes an overall expansion during maturation destroys the surrounding nucellus, and the now neighbouring innermost layer of the inner integument, by virtue of its cell size and alignment, simulates a condition to an epithelium. Thus, we are inclined to believe that what Sandt referred to as the "epithelium" of the nucellus should be identified with this layer of the inner integument.

The archesporial cell in the ovule arises in the hypodermal layer. As in the species reported by Warming (1878) and Sandt (1921), a parietal cell is cut off in the species investigated at present. The statements of Jönsson (1879–80, cited by Schnarf, 1931) and of Irmsches (1925) reporting the absence of a parietal cell in some species, in our opinion, need confirmation. The megaspore mother cell divider meiotically and gives rise to a linear tetrad of megaspores; the chalazal megaspore by three successive free-nuclear divisions builds up the embryo-sac. The antipodal nuclei degenerate before the maturation of the embryo-sac. In the species investigated by Sandt, the polar nuclei are reported to fuse as a result of the stimulus of the penetrating pollen tube. In *B. crenata*, however, we find that the secondary embryo-sac nucleus becomes fully organized long before the entry of the pollen tube into the micropyle.

We have been unable to demonstrate actual double fertilization; however, we presume that it takes place normally as evidenced by (*a*) the remains of the discharged pollen tube in the neighbourhood of the micropyle, and (*b*) the diploid and the triploid chromosome numbers in the cells of the embryo and of endosperm respectively.

After triple fusion, the primary endosperm nucleus moves towards the chalazal end prior to division. The first free-nuclear division takes place *in situ* (Text-Fig. 1). The daughter nuclei soon take their position at opposite poles (Text-Fig. 2). In this respect our observation is in conformity with that of Sandt (1921) to the extent that the endosperm development is *ab initio* nuclear. Although Sandt also mentions the later cellular nature of endosperm and the persistence of a single-celled layer of endosperm surrounding the mature embryo, his account is rather too brief. In *B. crenata*, the two daughter nuclei resulting from the division of the primary endosperm nucleus undergo simultaneous divisions and in the early stages of this phase, the derivatives of the respective nuclei tend to remain in micropylar and chalazal groups.

As compared between these two groups, the cytoplasmic accumulation in the chalazal region is relatively denser and the nuclei lie closer together (Text-Fig. 3). With subsequent free-nuclear divisions such a pattern becomes changed over to a condition where the nuclei become more or less equally spaced in a somewhat evenly distributed layer of peripheral cytoplasm (Text-Fig. 4). There is evidence to state that more free-nuclear divisions continue in the peripheral cytoplasm until 30 to 40 nuclei are formed. Now, each nucleus becomes isolated in a cubical mass of cytoplasm so as to give the appearance of individual



TEXT-FIGS. 1–6. Tissues of the ovule neighbouring the embryo-sac are not shown; all figures excepting Fig. 6 are from longisections of ovules. Fig. 1. Daughter nuclei of the primary endosperm nucleus, and two-celled proembryo. Fig. 2. A stage in the migration of the daughter nuclei to either poles. Fig. 3. Later stage of free nuclear endosperm showing chalazal and micropylar accumulation of cytoplasm. Fig. 4. Endosperm nuclei in peripheral cytoplasm. Fig. 5. Peripheral layer of endosperm cells. Fig. 6. Periclinal division of the peripheral endosperm layer as seen in transection of an ovule.

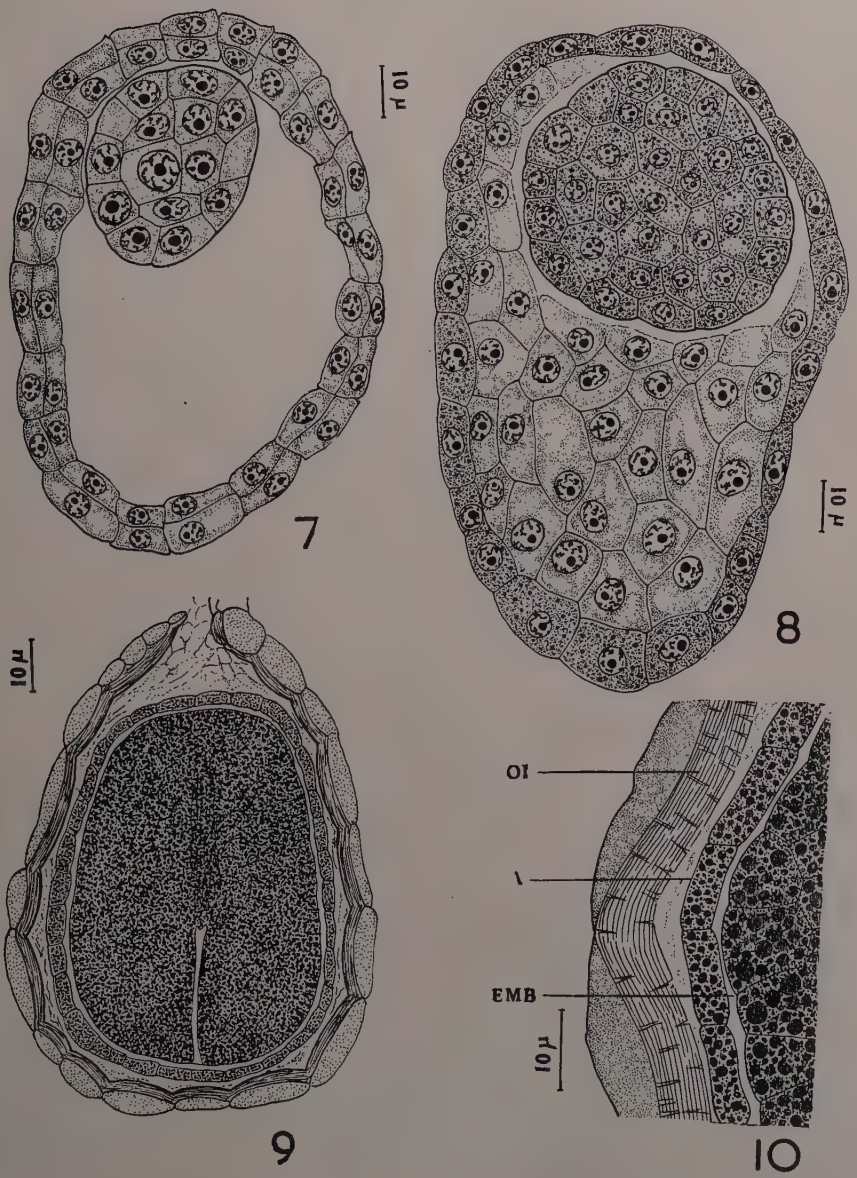
cells (Text-Fig. 5). No valid evidence could be gathered that the cleavages separating the ensheathing cytoplasm of the nuclei represent cell walls laid down through the activity of a phragmoplast. From this stage onwards the divisions in the endosperm are strictly cellular.

The single layer of peripherally arranged endosperm cells (Text-Fig. 5) undergoes a division in the periclinal plane (Text-Fig. 6). Thus, two peripheral cell layers of endosperm become organized (Text-Fig. 7). The outer layer of cells does not undergo further division. The inner layer of cells divides in diverse planes so as to fill the cavity (Text-Fig. 8). The developing embryo consumes the endosperm excepting the outermost layer. Even at the spherical stage of the proembryo (Text-Fig. 8) the outermost layer of the endosperm begin, to exhibit histological characters similar to the cells of the embryos in that oil droplets and aleurons become deposited in the cells in contrast to the remaining cells of the endosperm. That this layer should persist in the mature seed without being consumed by the developing embryo becomes significant from the point of view of function. In grasses, the presence of an aleurone layer is a common feature. While it is realized that at the present state of our knowledge it is difficult to attribute a cogent function to and recognize the method of functioning of this layer, it may be assumed that its morphological nature is similar to the aleurone layer met with in the seeds of many cereals. The similarity is most significant in the origin of this layer and its histological characters.

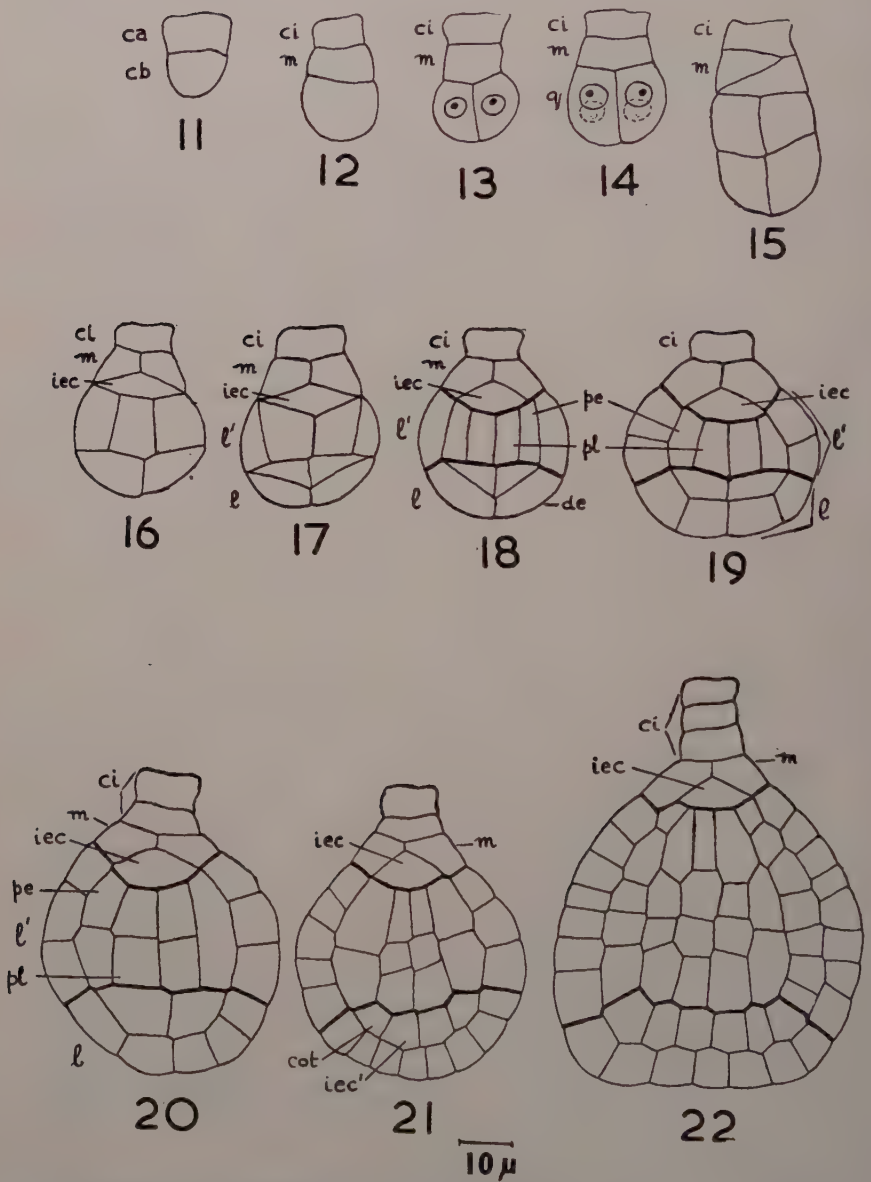
In the mature seed, the fully differentiated embryo fills the cavity, which is lined by the aleurone layer. The outermost cell layer of the outer integument alone persists as the seed-coat (Text-Figs. 9 and 10). The cells of this layer become highly modified in structure. They expand enormously in surface area and heavy lignin lamellæ are deposited on the inner periclinal wall in which numerous simple pits are scattered; the outer wall remains thin and an amber-coloured substance fills the cell lumen (Text-Figs. 9 and 10).

The sequence of developmental stages in the embryogeny of *Begonia crenata*, in all essentials, follows the *Onagrad* Type as described by Souèges (1939) for *Begonia semperflorens*. The differences are only quantitative and result due to precocious or accelerated divisions of some of the cells in the typical sequence to be described below.

The fertilized egg divides in a plane at right angles to the longitudinal axis of the embryo-sac (Text-Fig. 11). Thus a basal cell (*cb*) and a terminal cell (*ca*) are formed. The basal cell next undergoes a transverse division. The superior cell derivative (*m*) is the mother cell giving rise to the hypophysis (Text-Fig. 12). The terminal cell undergoes a vertical division (Text-Fig. 13). This division is immediately followed by a division at right angles to the previous one. Thus a quadrant is produced (Text-Fig. 14). The cells of the quadrant then divide in a transverse plane giving rise to the octant (Text-Fig. 15). The superior tier of the octant (*l*) divides in a tangential plane, the



TEXT-FIGS. 7–10. All figures are from longisections of ovules. Fig. 7. Two-layered endosperm with central cavity. Fig. 8. Differentiation of aleurone layer and the cavity filled with endosperm cells. Fig. 9. Longisection of a mature seed. Fig. 10. A part of the peripheral layers of the seed enlarged. A: aleurone layer; EMB: embryo; OI: Outermost layer of the outer integument forming the seed-coat.



TEXT-FIGS. 11–12. Stages in the development of the embryo. For details see text.

outer cell derivatives contributing to the formation of the epidermis (dermatogen) (Text-Fig. 17); the inner ones later divide vertically (Text-Fig. 21). The peripheral cells of the hypodermal tier (*cot* in

Text-Fig. 21) thus formed constitute the initials of the cotyledons, while the central cells of this tier (*iec'*) function as the initials of a part of the stem apex. The products of division of the epidermis contribute to the partial formation of the cotyledons, while the derivatives of the superficial layer of the inferior tier (*l'*) contribute cells to the organization of the hypocotyl (Text-Fig. 19). The inferior octant (of the stage illustrated in Text-Fig. 15) divides vertically at first separating an epidermis (Text-Figs. 16 and 17), then the periblem (*pe*) and the plerome (*pl*) (Text-Fig. 18). The cells of these histogens multiply in a regular fashion towards the construction of the fundamental tissues of the embryo (Text-Figs. 20, 21 and 22). The periblem and plerome are always seen distinctly.

The mother cell of the hypophysis (*m*) (in Text-Figs. 12–14) divides in a diagonal plane giving rise to the hypophysis, which functions as the initial (*iec*) of the root tip and the root cap. The inferior cell (*ci*) may build up a rudimentary suspensor, which later becomes crushed by the developing embryo. In fully mature embryo the cotyledons are well developed. This particular sequence of embryo development is considered as belonging to the *Lythrum* variation of the *Onagrad* type by Johansen (1950).

Summary

Some aspects in the embryology of a species of *Begonia* collected in the rain forests of Kerala and provisionally identified as *B. crenata* have been described. Deviations from the exomorphic features of the typical *B. crenata*, found in the species investigated at present, have been noted.

The microspores are formed by simultaneous division of the microspore mother cells followed by furrowing. The tapetum is binucleate and is of the secretory type. The pollen grains are shed at the two-celled stage.

The ovule is tenuinucellate and bitegmic. The archesporial cell cuts off a parietal cell. The development of the female gametophyte conforms to the *Polygonum* type. The antipodal nuclei degenerate and the polar nuclei fuse before fertilization.

The endosperm is *ab initio* nuclear. The nuclei formed after the first two or three divisions tend to occur at either pole in equal numbers imbedded in dense cytoplasmic accumulations. With further divisions, the nuclei become more or less evenly distributed in a peripheral layer of cytoplasm. When 30 to 40 nuclei are formed the endosperm becomes cellular. The outer layer which arises as a result of the periclinal division in the cells, later differentiates as the persisting aleurone layer, while the derivatives of the inner layer divide further so as to fill in the cavity with cells. The embryo absorbs all the endosperm excepting the aleurone layer.

The development of the embryo follows the *Lythrum* variation of the *Onagrad* type. In the mature seed the embryo fills the cavity

and the modified cells of the outermost layer of the outer integument constitutes the seed-coat.

Acknowledgement

We are thankful to our colleague, Sri. E. Govindarajulu, for assistance in the taxonomic analysis of the species.

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MEIOSIS IN AN AUTOTETRAPLOID RACE OF *ASPARAGUS RACEMOSUS* WILLD.

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Introduction

Cytological information on the large genus *Asparagus* (Liliaceæ) comprising about three hundred species (Willis, 1951) is restricted to a record of chromosome numbers for twelve species (Listed by Darlington and Wylie, 1955) and a few details of meiosis in *A. officinalis* worked out by Flory (1932). Recently Sharma and Bhattacharya (1957) have made a study of the karyotypes in *A. racemosus*, *A. plumosus*, *A. nanus* and *A. sprengeri*. These authors have confirmed the previous reports on chromosome numbers for *A. plumosus* and *A. sprengeri* and recorded new numbers for *A. racemosus* and *A. nanus* as $2n = 20$ for both.

The present paper deals with the study of meiosis in *A. racemosus* Willd., the common wild *Asparagus* occurring at Waltair. It showed a gametic number of twenty chromosomes, hence it is a tetraploid in relation to the basic chromosome number as well as to the number reported in the material described by Sharma and Bhattacharya (1957). Its meiotic behaviour has been worked out and presented below.

Material and Methods

Flower-bud material was collected from a few plants in the Andhra University Campus and Waltair during the monsoon of 1954–55. Acetocarmin squash preparations of young flower-buds were made after fixation in freshly prepared 1 : 3 acetic alcohol for twenty-four hours.

Observations

Information on the chromosome behaviour during meiosis with respect to association and chiasma formation have been gathered at diakinesis, this being the only stage analysable. Multivalent associations are formed and the number of quadrivalents, trivalents, bivalents and univalents formed varied widely from cell to cell. Table I shows the data regarding the chromosome association as obtained from an analysis of twenty nuclei at diakinesis. From this data it can be seen that (*a*) the number of quadrivalents varies from six down to one per cell and (*b*) that the average quadrivalent, trivalent, and univalent frequencies are 4·02, 0·35 and 0·405 per nucleus respectively. Text-Figure 1 shows a cell at diakinesis with six quadrivalents (the maximum

number per nucleus observed) and Text-Figs. 2, 3, 4, 5 and 6 show cells at diakinesis with 5, 4, 3, 2 and 1 quadrivalents respectively.

TABLE I

Chromosome association at diakinesis in A. racemosus

Association				No. of Cells
IV*	III	II	I	
6	1	6	1	1
6	..	8	..	1
5	1	8	1	1
5	..	10	..	5
4	1	10	1	1
4	..	12	..	5
3	1	12	1	1
3	..	14	..	2
3	..	13	2	1
2	2	12	2	1
1	1	16	1	1
		TOTAL	..	20

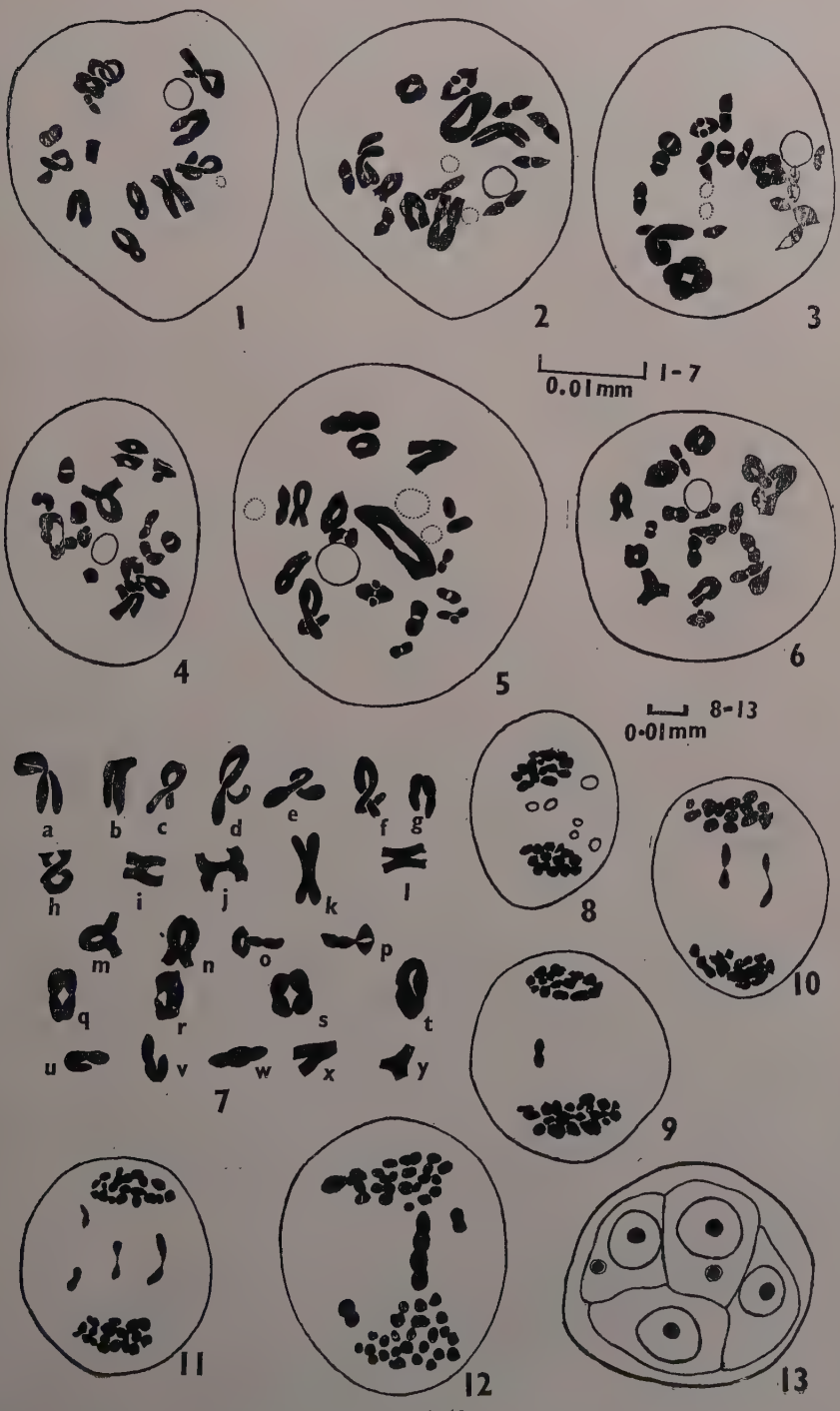
* IV = Quadrivalent; III = Trivalent; II = Bivalent; and I = Univalent.

Of the twenty types of quadrivalents and ten types of trivalents that can be expected to be formed in an autotetraploid organism with complete terminalisation (Darlington, 1931, 1937), quadrivalent types 11, 13, 15, 16 and 17 have been frequently observed in *A. racemosus*. The frequencies of the various types of multivalents are given in Table II. Text-Fig. 7 shows the various multivalent association types observed in the present study.

TABLE II

Frequency of types of multivalent associations at diakinesis in A. racemosus

Type	Trivalents		Quadrivalents				
	7	8	11	13	15	16	17
Number observed	4	3	28	10	5	3	30
Per cent. ..	57·14	42·85	36·84	13·16	6·59	3·94	39·47



TEXT-FIGS. 1–13.

TEXT-FIGS. 1–13. *Asparagus racemosus* Willd. Fig. 1. Diakinesis showing six quadrivalents, one trivalent, six bivalents and one univalent. Fig. 2. Diakinesis showing five quadrivalents and ten bivalents. Fig. 3. Diakinesis showing four quadrivalents and twelve bivalents. Fig. 4. Diakinesis showing three quadrivalents, thirteen bivalents and two univalents. Fig. 5. Diakinesis showing two quadrivalents, two trivalents, twelve bivalents and two univalents. Fig. 6. Diakinesis showing one quadrivalent, one trivalent, sixteen bivalents and one univalent. Fig. 7. Shapes of multivalents observed at diakinesis; *a* to *h*, shapes of quadrivalent type 11; *i* to *l*, shapes of quadrivalent type 13; *m* and *n*, shapes of quadrivalent type 15; *o* and *p*, shapes of quadrivalent type 16; *q* to *t*, shapes of quadrivalent type 17; *u*, *v* and *w*, shapes of trivalent type 7; *x* and *y*, shapes of trivalent type 8. Fig. 8. Anaphase I showing six lagging univalent chromosomes. Figs. 9–11. Telophase I showing one, two and four lagging chromosomes. Fig. 12. Telophase I with a non-disjoining chain type quadrivalent on the spindle. Fig. 13. A pollen tetrad with two micronuclei.

The total number of chiasmata per nucleus varies from 34 to 40, the average chiasma frequency per nucleus being 36·93 (Table III).

TABLE III

Frequencies of the cells at diakinesis showing different numbers of chiasmata in A. racemosus

No. of chiasmata per cell	No. of cells
34	1
35	3
36	2
37	3
38	4
39	0
40	2
TOTAL ..	15

Terminalisation coefficient is high, being 0·904. Therefore in most of the chromosomes terminalisation of the chiasmata is completed by the time they enter upon the diakinesis. The distribution of the chiasmata in the various chromosome associations is presented in Table IV.

TABLE IV

Distribution of chiasmata in the various chromosome associations at diakinesis in A. racemosus

No. of chiasmata	Uni-valents	Bi-valents	Tri-valents	Quadri-valents	Total No. of chias-mata
0	9	..	..	..	..
1	..	8	..	..	8
2	..	158	7	..	330
3	..	5	..	29	102
4	..	..	..	27	108
5	..	..	..	..	..
6	..	..	..	1	6
TOTAL ..	9	171	7	57	554
Total No. of Chromo-somes ..	9	342	21	228	600

The following types of meiotic abnormalities have been encountered in general: (1) Univalent formation at diakinesis, metaphase and anaphase I due either to failure of chiasmata or premature disjunction of bivalents (Text-Fig. 8); (2) formation of lagging chromosomes at anaphase and telophase I (Text-Figs. 9, 10 and 11); (3) formation of micronuclei in the pollen tetrads (Text-Fig. 13); and (4) formation of bridges at anaphase I due to persistent interstitial chiasmata in a bivalent or the presence of a non-disjoining chain type quadrivalent (Text-Fig. 12).

Up to 25% of the mature pollen grains showed shrinkage and were dead.

DISCUSSION

At meiosis the forty chromosomes were observed to be regularly going into trivalent and tetravalent associations. Quantitative data with respect to chromosome association, frequency of various types of multivalents and chiasma formation have been gathered at the diakinesis stage only. On an average 4·02 quadrivalents, 0·35 trivalents and 0·405 univalents per nucleus were observed. Similar data were recorded previously in organisms like *Allium* (Levan, 1937, 1940), *Hordeum* (Peto, 1936), *Agropyron* (Myers and Hill, 1942), *Zea mays* (Kadam, 1944; Venkateswarlu, 1950), *Lycopersicum* (Upcott, 1935). *Brassica* (Howard, 1939), *Oenothera* (Linnert, 1948) and several others. Quadrivalent types 11, 13, 15, 16 and 17 were observed during the present study, types 11 and 17 being most frequent. The occurrence

of these latter types at diakinesis requires the formation of a single partner exchange and three chiasmata at least (one in each arm) for type 11 and one chiasma for each of the four arms for type 17 at pachytene (see Linnert, 1948). For the formation of these two types of diakinesis association chromosomes with median or sub-median centromeres will be more favourably suited and therefore an analysis of the karyotype and if possible of the pachytene chromosomes can be expected to show a high frequency of these chromosome types. In fact, Sharma and Bhattacharya (1957) have actually observed the presence of six pairs of median and four pairs of sub-median chromosomes in the somatic complement of the diploid material of the same species.

The basic chromosome number for the genus *Asparagus* as reported by Darlington and Wylie (1955) is ten. The species *A. racemosus* whose meiotic behaviour is reported here shows a chromosome number of $n = 20$. Sharma and Bhattacharya (1957) have earlier reported a chromosome number of $2n = 20$ for the same species. The forty chromosomes of the present material were seen to be regularly entering into multivalent associations during meiosis. This and the behaviour during the post-metaphase stages leads to the supposition that the present material is autotetraploid and probably an autotetraploid race of the diploid species. A perusal of the chromosome numbers of the species of the genus *Asparagus* so far reported (listed by Darlington and Wylie, 1955) clearly shows that polyploid series occur in the various species of the genus. The present report of a natural autotetraploid race of *A. racemosus* shows that polyploidy has a role to play in the intraspecific differentiation of the genus also. This is further supported by the fact that Randall and Rick (1945) have reported in the populations of another species, *A. officinalis*, the occurrence of triploids trisomics, haploids and tetraploids as members of twin seedlings arising out of polyembryony. Double seedlings have been observed by the present author in *A. racemosus* also and it is possible that phenomena similar to that observed in *A. officinalis* might be responsible for the origin of the polyploid race described here.

Summary

An autotetraploid race of *A. racemosus* has been observed and its meiosis with reference to chromosome association and chiasma formation has been studied. Frequency of multivalents, frequency of the various types of multivalents and chiasma frequency have been gathered and presented. The usual meiotic aberrations common to autotetraploid organisms have been recorded. A possible way of origin of the polyploid race is given.

Acknowledgements

I have great pleasure in acknowledging my sincere thanks to Professor J. Venkateswarlu, D.Sc., Ph.D. (Cantab.), F.A.Sc., F.B.S., Professor and Head of the Department of Botany, Andhra University, Waltair, for suggesting the problem and for guidance. My thanks are also due

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ON *GASTROCLONIUM IYENGARII* A NEW SPECIES FROM INDIA

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Since Kützing established the genus *Gastroclonium* in 1843, a number of species have been ascribed to the genus by various authors. Out of these, only three species of *Gastroclonium* are recognised, *viz.*, (1) *G. clavatum* (Roth.) Ardiss. (= *Lomentaria clavata* J. Ag., *G. salicornia* Kütz., *Chylocladia clavata* Bliding), (2) *G. ovale* (Huds.) Kütz. (= *Lomentaria ovalis* J. Ag., *Chylocladia ovalis* Harvey, *G. umbellatum* Kütz.), and (3) *G. coulteri* (Harv.) Kylin (= *Lomentaria ovalis* var. *coulteri* Harv., *L. ovalis* var. *robustior* J. Ag.). These three species have been known only from the Atlantic, the Mediterranean and the Pacific. The genus *Gastroclonium* has not been recorded from India so far.

In February 1955, the author collected at Okha on the western coast of India a *Gastroclonium* which appears to be new and quite different from the three previously known species of *Gastroclonium*. An account of this alga is given here below.

The alga was collected during low tide from a trough-like depression below low water mark. It was found growing usually with *Halimeda tuna* (Ell. and Sond.) Lamx.

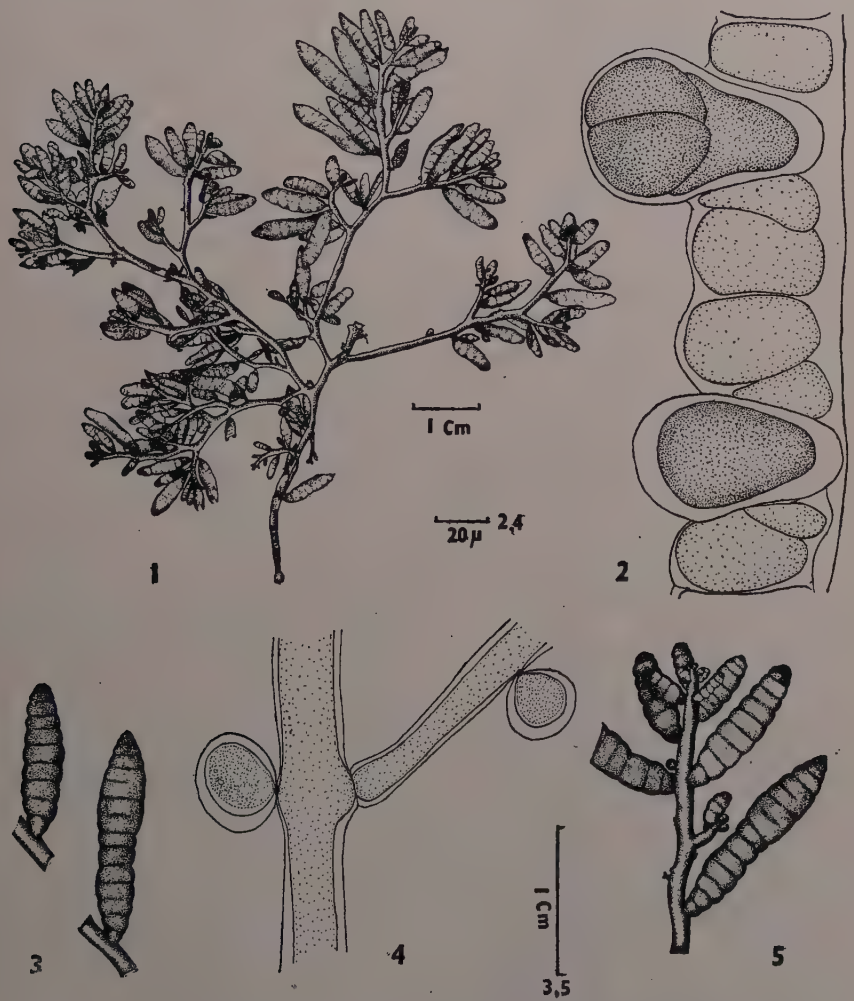
It has a branched prostrate portion by which it is attached to the substratum and from which arise a number of erect shoots. These erect shoots arise close to each other and give a densely packed appearance. The erect shoots reach a height of 10 cm. (Plate IV, Figs. 1–3).

The rhizome and the erect shoots are cartilaginous and cylindrical. The erect shoots measure about 2 mm. in thickness. These are generally dark-brownish pink in colour with a shade of green to light-red at the extremities and free ends. The rhizome and the erect shoots are solid throughout. In a cross-section of the shoot, the cells near the periphery are small while those towards the centre are large in size and comparatively thin-walled. In longitudinal section, the cells in the central portion are elongated along the longitudinal axis of the shoots.

The upper portions of these erect shoots bear a number of ramuli, while the lower portions are comparatively naked. The several ramuli which are laterally disposed on the axis present a more or less tufted

appearance. Secondary ramuli are generally absent, but are occasionally present, and then they are rudimentary only. Generally speaking the ramuli are developed in acropetal succession (Text-Fig. 5). They are 15–20 mm. long, rarely longer, and 2·5–3·5 mm. broad, membranous and soft. Their colour varies from red to pink while young and light-red or purple with shades of light-green when old.

Unlike the axis bearing them, the ramuli are hollow structures. The very young ramuli are spherical to more or less clavate with a



TEXT-FIGS. 1–5. *Gastroclonium iyengarii* sp. nov. Fig. 1. Habit ×1. Fig. 2. A portion of the wall of the ramuli showing single layer of cells and tetrasporangia, ×295. Figs. 3 and 5. Ramuli showing the number of segments. ×2. Fig. 4. Bulb cells ×325.

broadly rounded apex and an attenuated base (Text-Fig. 5). As they grow older they become longer and more or less inflated. The central cavity of the ramulus is, however, interrupted at more or less regular intervals by well-developed diaphragms. The diaphragm is single layered throughout. The fully developed ramuli are linear oblong, with a narrowed base and a more or less acute apex, and are moderately to deeply constricted at the diaphragms and appear articulated into a number of segments (Text-Figs. 3, 5; Plate IV, Fig. 1). The wall of the ramuli is one cell thick (Text-Fig. 2). The number of segments vary from 11–20 in each. The segments are longer in the middle portion of the ramulus (95–135 μ long), but are shorter towards the basal (50–80 μ long), and the distal ends (13–40 μ long). The lowermost segment is the shortest of the basal segments (Text-Figs. 3, 5; Plate IV, Fig. 1).

The apical region of the ramuli, seen from above, shows about 10–12 apical cells with an equivalent number of radiating filaments diverging from a central point. The hollow cavity of the ramuli also shows the axial filaments with bulb-cells characteristic of the group (Text-Fig. 4). The axial filaments are from 16·5–30 μ across and the bulb-cells are 23–33 μ long and 20–26 μ broad.

The alga is encased as it were in a firm mucilaginous envelope throughout. This envelope usually is only about 16·5 μ thick though in places it is up to 36 μ or even more in thickness. It shows on its outer side a definite cuticle. A mucilage envelope of a similar nature has been described for *Gastroclonium ovale* (= *Lomentaria ovalis*) by Grubb (1925, p. 189) and for *Chylocladia kaliformis* by Kylin (*see* Fritsch, 1945, p. 513).

No sexual plants were observed. Tetrasporic plants were, however, found in the collection. The formation of tetrasporangia and tetraspores are similar to those described by Bliding (1928) in *Gastroclonium ovale* (= *Chylocladia ovalis*). The tetrasporangia are pyriform in shape and are about 100 × 50 μ in size (Text-Fig. 2).

Discussion

The Indian alga differs from all the three species of *Gastroclonium* as defined and recognised by Kylin (1931), *viz.*, *G. ovale*, *G. coulteri* and *G. clavatum*. It is characterized by (1) the larger number of segments of the ramuli, (2) the absence or very rare occurrence of secondary ramuli, (3) the lowermost segment of the ramulus being the smallest of the basal segments, (4) the acute apices of the ramuli and (5) the more robust nature of the ramuli. It differs from *G. clavatum* in the general appearance of the ramuli, in the shape of the ramuli being not lanceolate but linear-oblong with narrowed ends and in the usual absence of secondary ramuli. It differs from *G. ovale* in the shape of the ramuli, in the larger number of segments of the ramuli and in the basal segment being very short. It differs from *G. coulteri* in the shape and size of the ramuli, in the larger number of segments of the ramuli and in the wall of the ramuli being only one cell thick and not three cells

thick (*see* Smith, 1938, Fig. 187 B). It resembles to a certain extent the alga from Japan which Okamura (1907–09) described as *Gastroclonium ovale*. Dawson (1950) transferred this Japanese alga of Okamura to the genus *Cœloseira* of Hollenberg (1940), which has a habit more or less similar to that of *Gastroclonium* and referred it to *C. pacifica* Dawson. The genus *Cœloseira* rests essentially on the common occurrence of polyspores in it as against the tetraspores commonly seen in *Gastroclonium*, though polyspores have occasionally been reported in the latter genus also (*see* Smith, 1938, p. 342). The Japanese alga has both polyspores and tetraspores. But the present alga has only tetraspores and so is here referred to the genus *Gastroclonium*. Again in the nature of the basal segments also, the present alga differs from the Japanese alga. According to Okamura the basal segment in the Japanese alga is longer than the remaining ones, whereas in the present alga the lowermost segment is the shortest among the basal segments. The author therefore considers that the present alga is a new species of *Gastroclonium*. He has great pleasure in naming the alga *Gastroclonium iyengarii* sp. nov., after Professor M. O. P. Iyengar as a token of the author's respects and regards for him.

Diagnosis of Gastroclonium iyengarii *sp. nov.*

Frond cartilaginous, erect, cylindrical, 2 mm. thick, dark-brown in the older parts, light-green to light-red at the extremities; branching pseudodichotomous; frond generally naked below and bearing above a number of ramuli, laterally disposed in acropetal succession. New ramuli frequently developing from older portions of the fronds also. Ramuli inflated, linear-oblong, with a narrow base and a more or less acute apex; membranous, soft, 15–20 mm. long. and 2·5–3·5 mm. broad. Ramuli segmented; number of segments varying from 11–20 in each, segments in the middle portion of the ramuli longer than those in the basal and in the distal parts, the lowermost segment being the shortest among the basal segments. Colour of ramuli varying from red to pink in young ones and light-red or purple with shades of green in older ones. Wall of ramuli only one cell thick. Cavity inside the ramuli intercepted by diaphragms at intervals. Segments in the middle portion of the ramuli, 95–135 μ long, at the basal portion 50–80 μ long and at the distal portion 13–40 μ long. Secondary ramuli generally absent, but occasionally present and, when present, rudimentary. Axial filaments of ramuli 16·5–30 μ across, bulb-cells 23–33 μ by 20–26 μ. Mucilage envelope uneven, usually 16·5 μ thick and occasionally up to 36 μ thick or even more in places. Male and female reproductive structures not known. Tetrasporangia present, tetraspores being formed by tetrahedral division.

Habitat.—Type collected growing on rocks below low water mark in open gulf in a shallow trough-like depression, on substrata of small rocks and boulders covered by fine sand, Okha Port, India, February 20, 1955, No. 3421 deposited in the Herbarium, Indian Museum, Calcutta. Iso-type, No. 3422, from same locality deposited with the type at Calcutta. Para-type, January 6, 1955, Okha, in Herbarium

M. O. P. Iyengar, and deposited in the Herbarium, Madras University Botany Laboratory, Madras.

Latin Diagnosis

Gastroclonium iyengarii *spec. nov.*

Frondes cartilaginaceæ, erectæ, cylindricæ, 2 mm. crassæ, in partibus vetustioribus fusce brunneæ, pallide virides vel pallide rubræ ad apices, ramis pseudo-dichotomis, vulgo nudæ infra, supra supportantes ramulos quosdam, qui lateraliter dispositi sunt successione acropetala. Ramuli novelli sæpe emergentes ex partibus quoque vetustioribus. Ramuli tumescentes, lineari-oblongi, basi angustata, apice plus minusve acuto, membranacei, molles, 15–20 mm. longi, 2·5–3·5 mm. lati, segmentati, segmentorum numero 11–20 in singulis ramulis; segmenta in media parte ramulorum longiora quam in partibus basalibus vel ulterioribus, infima vero brevissima omnium segmentorum basalium. Ramuli rubrescentes vel rosacei in partibus junioribus, pallide rubri vel purpurascentes tinctione quadam viridi in partibus vetustioribus. Ramulorum parietes una cellula crassi; eorum vero cavitates diaphragmatibus ad intervalla interceptæ. Segmenta in parte media ramulorum 95–135 μ longa, in parte basali 50–80 μ longa, in parte apicali 13–40 μ longa. Ramuli secundarii sæpe nulli, nonnumquam vero adsunt, et tunc rudimentarii. Filamenta axialia ramulorum 16·5–30 μ diam.; bulbi cellulæ 23–33 $\times$ 20–26 μ. Mucilaginis involucrum inæquale, vulgo 16·5 μ crassum, nonnumquam vero usque ad 36 μ vel ulterius crassum alicubi. Partes reproductivæ masculinæ vel femininæ ignotæ. Tetrasporangia adsunt, tetrasporis efformatis per divisionem tetrahedram.

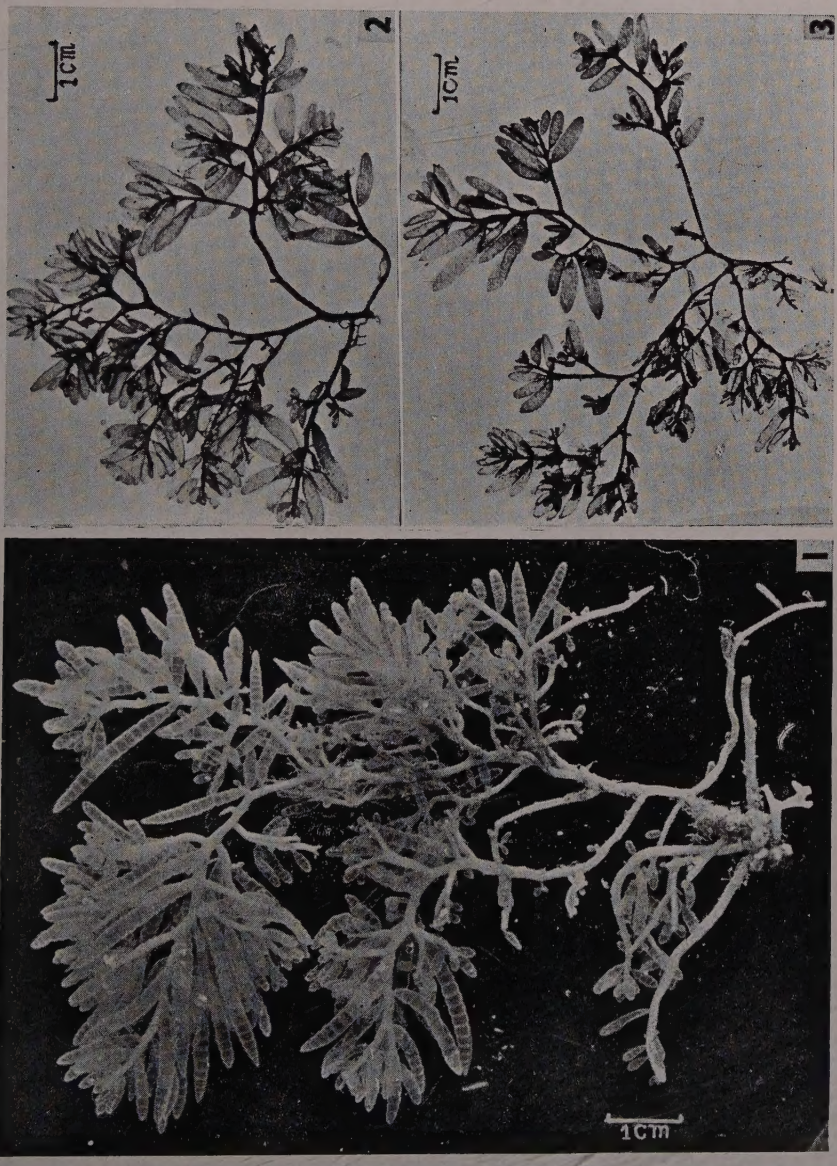
Typus lectus saxis fixus sub limite inferiore æstus marini ad Okha in Saurashtra die 20 februarii anni 1955 et positus in Herbario Musæi Indici ad Calcutta, sub numero 3421; Isotypus, No. 3422, lectus eodem die et loco ac typus, positus est in eodem Musæo Calcuttensi; paratypus lectus eodem in loco die 6 januarii anni 1955 e herbario M. O. P. Iyengar positus in Herbario laboratorii botanici universitatis Madraspatensis.

Summary

A new species of *Gastroclonium*, *G. iyengarii*, is described from Okha Port, on the west coast of India.

The Indian alga differs from the three previously described species (1) in the basal segment of the ramuli being much smaller than the upper ones, (3) in the size and shape of the ramuli, (3) in the larger number of segments of the ramuli and the absence of secondary ramuli generally.

Only tetrasporic individuals were observed. The tetraspores are tetrahedrally disposed.



K. S. Srinivasan

The writer expresses his grateful thanks to Prof. M. O. P. Iyengar for his kind help in the preparation of this paper and to Rev. Fr. H. Santapau for the Latin diagnosis. The writer also thanks the Director, British Museum, for the supply of a specimen of *G. ovale* for comparative studies and Dr. T. V. Desikachary, Madras, for providing beautiful material of the alga from his rich collection and for the habit photograph of the tetrasporic plant, illustrated in Plate IV.

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Explanation of Plate IV

Figs. 1–3. *Gastroclonium iyengarii* sp. nov. Fig. 1. Photograph of a tetrasporic plant preserved in fluid, ×1¼. Figs. 2 and 3. Photographs of herbarium specimens. nat. size.

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